

Behaviour of hybrid male *Tetrao tetrix* male × *T. urogallus* female on black grouse and capercaillie display grounds

Jan PORKERT¹⁾, Roar SOLNHEIM²⁾ & Arne FLOR³⁾

¹⁾ Na Slupi 12, CZ–128 00 Praha 2, Czech Republic

²⁾ Agder Museum of Natural History, PO Box 1018 Lundsiden, N–4602 Kristiansand, Norway

³⁾ Bergstien 18, N–4800 Arendal, Norway

Received July 28, 1997; accepted February 19, 1998

Published June 29, 1998

Abstract. The offspring of crosses between male black grouse (*Tetrao tetrix*) and female capercaillie (*T. urogallus*) are the most common grouse hybrids. Some male hybrids (F_1 generation) may be fertile and produce offspring (F_2 generation) with females of capercaillie, rarely, with black grouse. Specimens and descriptions of lekking behaviour are also available for probable F_3 and F_{-3} hybrids. We documented 3 and 2 male F_1 hybrids simultaneously displaying on a black grouse lek in Norway (1993–1997), and, solitarily displaying hybrids on black grouse lek in the Czech Republic (1960–64), in Sweden (1991–93) and Norway (1992, 1997). In 1996 and 1997 up to three hybrids were observed on a capercaillie display ground 2 km away from the first mentioned black grouse display ground. Mating with female capercaillie was observed in 1992 and 1994. We describe the hybrids' lekking behaviour and attitudes towards other tetraonids.

Lekking behaviour, backcrossing, grouse hybrids

INTRODUCTION

Hybrids between male black grouse and female capercaillie are the most common grouse hybrids, termed “rakkelhane” in Norwegian. Some male hybrids (F_1 generation) may be fertile and produce offspring (F_2 generation) with females of both capercaillie and black grouse. Skin material and descriptions of lekking behaviour also exist for probable F_3 and F_{-3} hybrids. Successively increased fertility is suspected through such backcrossing (Bergman 1940, Höglund & Porkert 1989, Porkert 1995a, Porkert et al. 1996).

Male F_1 hybrids usually occurs solitarily on black grouse display grounds, and act aggressively towards male black grouse. We have found three reports of collectively displaying hybrids. Crown Prince Rudolf (Anonymus 1883) mentioned 4 hybrids displaying on a capercaillie lekking ground in NE Bohemia, of which two supposed F_3 -hybrids were shot the same day (cf. Meyer 1887, Klaus et al. 1989, Porkert 1995a). Viht (1987) reported three hybrids displaying in 1971 and 1972 on a black grouse lekking ground with approximately 20 male black grouse in Estonia. Nystrom (1990) observed three male hybrids on a black grouse display ground in Sweden. Bjørn Bjerke (pers. com.) observed 2 hybrids and two female capercaillie on a black grouse display ground in 1985 in SE Norway. Here we describe lekking behaviour of hybrids based on our observations of solitarily (Czech Republic 1960–64, Sweden 1991–93, South-Norway 1992 and 1997) and collectively (South-Norway 1993–97) displaying hybrids on black grouse display grounds, and on a capercaillie display ground in 1996 and 1997.

METHODS

Hybrids displaying at the black grouse lek at Øvre Landvik were first documented by Arne Flor in 1992 (Flor 1993a, b). Jan Porkert and Roar Solheim took part in the observations from 1994 and 1995, respectively. Observations were made from blinds close to the displaying ground centers, and the birds' behaviour was documented by photography and video taping. Observation days and observed behaviour and interactions between different birds are given in Tab. 1 and 2. Terminology follows Hjorth (1970). In 1997 Asbjørn Lie contributed with one observation day.

RESULTS

During spring 1992 one hybrid was present on the black grouse lek in Øvre Landvik, S. Norway (Fig. 1), whereas during 1993 and 1994 there were 3 hybrids on this lek together with 3 male black grouse, which displayed in parts of the territories of the hybrids. In 1995, 1996 and 1997 the lek contained 2 hybrids and 1–3 male black grouse. In spring 1996 three other hybrids were observed 2 km away on a capercaillie lek with only one displaying male capercaillie. In 1997 one hybrid was displaying in the center of this display ground prior to the copulation period of the capercaillie. A second subordinated male capercaillie was also observed with a non-vocal display close to the center this year. Both capercaillie were dominantly aggressive towards the hybrid, chasing it away whenever it came too close to either of the capercaillies' respective displays centers. During the peak of copulation period, the hybrid's display center was located some 15–20 meters away from the dominant capercaillie. A hybrid (probably a second individual) displayed some 150–200 m north of the capercaillie's display center. One male hybrid (probably a third individual) was also seen on a black grouse display ground 1.1 km NW of the capercaillie lek (cf. Tab. 1 and 2, 1996 and 1997).

We have observed the following patterns of behaviour:

1. Wing-beat display

Upright and standing on ground without moving forward, similar to black grouse (Fig. 2, cf. Porkert et al. 1997: fig. 2, Hjorth 1970: fig 78).

Announcing with "drumming flight" similar to male capercaillie (Fig. 3, cf. Porkert et al. 1997: fig. 3, Hjorth 1970: fig. 58). Drumming flight may be reduced, and may lack vocal sounds or be performed with reduced sound (Porkert et al. 1997).

2. Thin-neck upright

This behaviour is commonly displayed on ground and in trees to demonstrate the dominance of the territory holder (Hjorth 1970). The hybrid cocks stand or slowly move in a posture very similar to the capercaillie thin-necked upright. (Fig. 4, cf. Porkert et al. 1997: fig. 4, Hjorth 1970: fig. 59).

The display song is an individually varying, recurring "crrrrs"-sound, the frequency is mostly 1–2 kHz, but even reaching approximately 4 kHz (Klaus et al. 1989: fig. 26).

3. Upright cum wingdragging, singing and tailtilting is similar to that in capercaillie

The tail is fully fanned and tilted 30–40° sideways towards the female or rival (Fig. 5, Porkert et al. 1997: fig. 6). The sideways tilting is more pronounced than in both capercaillie and black grouse (cf. Hjorth 1970: figs 63b, 64b, 84b; "black grouse never seen to exceed 15°").

4. Aggressive behaviour

Solitarily displaying hybrids are usually highly aggressive towards male black grouse, as documented in all articles describing observations of hybrids on black grouse leks. During the periode 1953–1987, while the extinction and behaviour of both capercaillie and black grouse was studied in Orlické hory Mountains in NE Bohemia, hybrids were present both before and during the disap-

Tab. 1 Observation days and periods on the black grouse lek at Øvre Landvik, showing behaviour of hybrid "rakkelhøner" towards conspecifics, female grouse and male black grouse. Explanations: 1 = no days; 2 = no rakkelhøner; 3 = no female capercaillie; 4 = no copulations; 5 = no female black grouse; 6 = no copulations; 7 = fights with male conspecifics - no days; 8 = aggression towards male black grouse - no days; * = data from second lek; see text

year, observation periode	1	2	3	4	5	6	7	8	notes	observer & no days
1992										
26.4	1	1	3	>2	0			0		AF 1
1993										
18.4.-4.5.	4	2-3	(1) ⁱ	0	(1) ⁱⁱ	0	0	4	i:heard 24.4. ii:heard 4.5.	AF 4
1994										
26.4.-5.5.	7	1	1 ⁱ	1 ⁱⁱ	0		5	6	i:29.4., 1.5. i, ii:5.5.	AF 4 JP 6
21.-23.5.	3	3-1	0		0		0	0	mostly quiet in territory	JP 3
30.9.	1	2	0		0		0	0	no activity 1.10.	JP 2
1995										
10.-14.4.	2	2	0		0		1	?		AF 2
22.4.-4.5.	8	2	1 ⁱⁱ (2?) ⁱⁱⁱ	0	1 ⁱⁱ (2) ⁱⁱⁱ 3 ⁱⁱⁱⁱ	0	?	1+? ⁱⁱⁱⁱ	i:24.4., ii:25.4. iii:26.4.;heard iiii:1.5.;invitation low activity	AF 6 RS 6
4.-7.5.	4	1-2	0		0		0	0	8.5; rain, no birds	JP 4
10.5.	1	2	0		0		0	0		RS 1
1996										
20.-26.4.	2	2	0		0		0	1		AF 2
3.-8.5.	6	2	0		3 ⁱ -1 ⁱⁱ	0	0	2 ⁱ	i:4.4.;invitation, fight ii: 5.& 7.4.:flew over the lek. 6.5.:invitation	JP 6
1997										
26.4.	1	2	0		0		0	0	males not simult. on lek. No. 2 low act.	AL 1
3.-4.5.	2	1	0		0		0	0	low act. only in tree	JP 2
4.5.*	1	1	0		0		0	0		AF 1

pearance of male capercaillies. This so called "rakkel"-phase (1959-64, Porkert 1990, 1995b) represent a special periode in the extinction phase of both species, caused by habitat degradation due to pollution and modern forestry (Porkert 1979, 1980, 1982, 1991a, b). In this period male black grouse, too, became more aggressive and started solitarily displaying (Porkert 1976). The male hybrid's aggression excluded normal black grouse display on or close to the lekking grounds. The same aggressive behaviour was observed on a black grouse lek with one male hybrid at the Grimsö Research Station in Sweden. After the hybrid cock turned up on this lek in 1991, female black grouse disappeared since 1992. In 1993, the hybrid male moved to another lek 1 km away. This is in contrast to our observations on the black grouse lek with collectively displaying hybrids at Øvre Landvik in S-Norway, where a two-level hierarchy between hybrids and male black grouse developed (Porkert et al. 1997). The male hybrids had fixed territories according to their individual status (Fig. 1). Male black grouse were allowed to display at close distance when they stayed at the secondary parts of the display ground, sitting in trees or in the thick heather vegetation.

Head and neck "bowing", with a modulated display sounds is the slightest form of aggressive behaviour, resembling wide-necked attitudes cum belching cantus in capercaillie (Porkert et al. 1997: fig. 7, cf. Hjorth 1970: fig. 64).

Fighting with wings beats and/or pecking between hybrids is similar to capercaillie's fighting behaviour (Hjorth 1970: figs 65, 67), and is initiated and occasionally terminated with deep bowing (Porkert et al. 1997: fig. 8) of both rivals. Dominance is terminated through beak fighting (Porkert et al. 1997: fig. 9) or wing beat fighting (Porkert et al. 1997: fig. 10). This fighting behaviour is mostly observed between the hybrids themselves. Fight between a hybrid and the subordinate capercaillie was observed on April 20, 1997 (Tab. 2). Male black grouse avoid confrontations with hybrids by fleeing (Porkert et al. 1997).

5. Matings

Matings with female capercaillie were observed on April 26, 1992 (AF) and on May 5, 1994 (JP, Fig. 7, 8). In 1992 the single present male hybrid (probably one years old, cf. Porkert 1995a, according to plumage characters) was mating several times with two female capercaillies (Flor 1993a, b). In 1994, one female capercaillie was observed on the lek, and mating was seen only once. The hybrid mated like male capercaillie (Fig. 8, cf. Fig. 9, Porkert et al 1997: fig. 12, and Höglund 1957, Couturier & Couturier 1980: pl. LX, Klaus et al. 1989: fig. 39), now and then with a few wingbeats like male black grouse (cf. Porkert 1996, Porkert et al. 1997: fig. 13, and Hjorth 1970: fig. 85, Klaus et al. 1990: figs 28, 29).

On May 1, 1995 and on May 4 & 6, 1996, 1–3 black grouse females were observed inviting to mate. The invitations were probably directed as well to a male black grouse, which was displaying 3–5 m behind the displaying hybrid (Porkert et al. 1997).

Our observations show that in a choice between male hybrids and male black cocks, a female capercaillie prefers to mate with hybrids, whereas a female black grouse prefers to mate with their own species.

On April 20 & 23, 1997, 3 and 6 copulations, respectively, were observed between the dominant capercaillie male and the females. A total of 5 and 8 hens, respectively, were observed on the display center on these two mornings (Fig. 9). In 1996 the observation tent was placed too close to the mating center of the capercaillies, thus forcing the birds to copulate some 20 meters away.

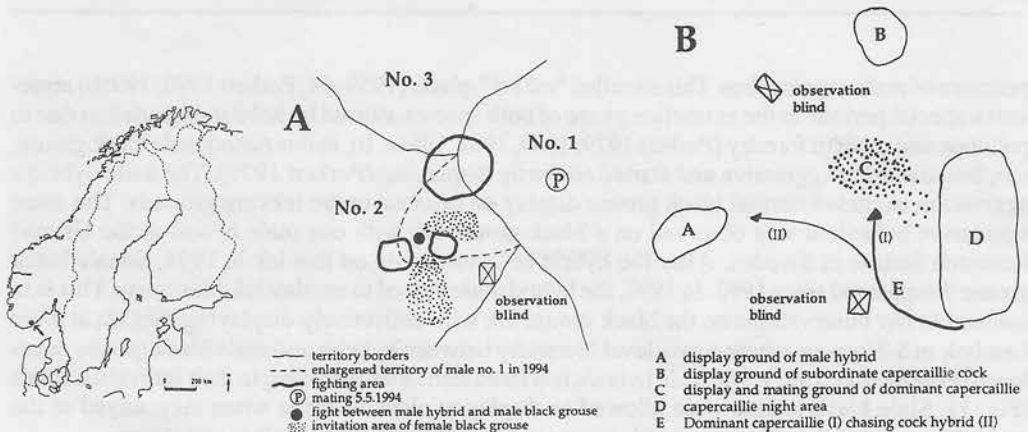


Fig. 1. The location of both the black grouse (A) and the capercaillie (B) display grounds in Øvre Landvik, South Norway, with the territories of the hybrids and the capercaillies.

Tab. 2 Observation days and periods on the capercaillie lek at Øvre Landvik, showing behaviour of both hybrid "rakkelhane" and capercaillie males and females. Explanations: 1 = no days; 2 = no rakkelhane; 3 = no male capercaillie; 4 = no female capercaillie; 5 = no copulations; 6 = fights with male conspecifics - no observ.; 7 = fights with male capercaillies - no observ.; 8 = fights between capercaillies - no observ.; 9 = capercaillies aggression towards hybrids

year observation periode	1	2	3	4	5	6	7	8	9	notes	observer & no days
1996											
27.4.	1	3	1	5-6	0						AF 1
1.5.	1	1	1	0	0	2	0	0	0		AF 1
9.5.	1	1	1*	0	0	0	0	0		*:only heard	AF, JP 1
21.10.	1	1*								*:only heard	JP 1
1997											
26.3.	1	1	0	0							AF, RS 1
2.-3.4.	2	1	0	0	0	0	0	0			JP 2
13.4.	1	1	1(+1)*	1	0	0	0	0		*:only heard	AF 1
20.4.	1	1	1+1*	5	3	0	1+4*	>3	>4	*:subordinate male	AF 1
23.4.	1	1	1+1	8	6	0	0	>2	>3		AF, RS 1
24.4.	1	0	0	0							RS 1
26.4.	1	0	1	0						birds disturbed by people at 05.00	AF, RS 1
30.4.-2.5.	3	1*	1	0	0	0	0	0	0	*:only heard	

mating center was occupied by the displaying cock hybrid. When the tent was placed at an acceptable distance in 1997, the hybrids was driven away from the original copulation center by both capercaillie males (see map, Fig. 1).

DISCUSSION

Although the hybrid "rakkelhane" was described as early as 1744 (Rutenschiöld in Meyer 1887), and there are many literature reports on hybrids occupying both black grouse and capercaillie display grounds, the hybrids' behaviour has hitherto been fragmentarily described. This is quite contrary to the comprehensive literature on both black grouse and capercaillie (Hjorth 1970, Klaus et al. 1989, 1990, Koivisto 1965, Kruit & Hogan 1967). Here we have described the behaviour of the hybrids according to the terminology used by Hjorth (1970). For a full description of the behaviour patterns, see Porkert et al. (1997).

Contrary to E. Viht's (1987) observations of the female capercaillie which "invited male black grouse only... and was supposed mother of hybrids" on a black grouse display ground with 3 male hybrid "rakkelhane" in Estonia, no female capercaillie that visited the lek at Øvre Landvik showed any interest for black grouse males (Porkert et al. 1997).

Unfortunately we have been unable to document any F₂-hybrids resulting from the copulations we have observed between hybrids and female capercaillies. This is probably due to at least some of the copulations documented in 1992 (Flor 1993 a, b) being unfulfilled. Both the females capercaillies' repeated invitations and the hybrid male's low age (probably a one year old bird cf. Porkert 1995a for plumage characters) support this interpretation. Contrary to this, the female capercaillie's behaviour on 4 May 1994, indicate a successful copulation with the dominant hybrid (Porkert et al. 1997). However, due to the variable fertility of the hybrids, production of a F₂-generation depend on the sperm quality of the respective male hybrid involved (Höglund & Porkert 1989, cf. Porkert 1995a, Porkert et al. 1996).

E. Viht (1987) pointed out that "female black grouse kept close to male black grouse only", but gave no further information on the relations between females and male hybrids during hens' visit at the lek. Our observations showed that female black grouse exclusively invited male black grouse for mounting. However, due to the presence of the male hybrids, male black grouse were deterred from mating (Porkert et al. 1997). Whereas Hjorth (1994) reports great turbulence on black grouse leks visited by male hybrids, our observations both in NE-Bohemia and in central Sweden show that the aggressiveness of male hybrids did not allow any close presence of male black grouse at all. Only when a highly receptive black grouse hen appears on such a lek occupied by a male hybrid, without any male black grouse present, a successful copulation might be achieved. Thus supposed F₂-hybrids between male hybrid and female black grouse as reported in literature (Meyer 1887, Klaus et al. 1989, Porkert et al. 1996), must be extremely rare. Additional reasons for this are: 1. Copulation by hybrid male with black grouse female may be somewhat more difficult owing to the size difference between the sexes (cf. male capercaillie × female black grouse in the breeding experiment, Höglund & Porkert 1989); 2. Eventually the sperm quality of the respective male hybrid is essential for production of a potential F₂-progeny.

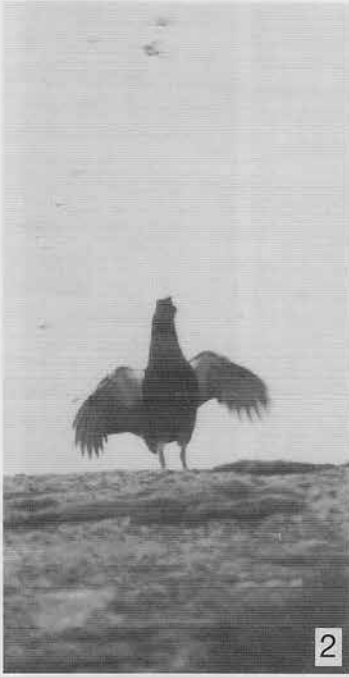
As male hybrids show variation in character, display sounds and probably also fertility (Höglund & Porkert 1989, for weight of testes, see Tab. 2, and unpubl. Data for histology), there is also individual variation in behaviour. We were able to recognize individual male hybrids based on differences in white spots on under-tail coverts and secondaries, on glossy colour and length of tail feathers, as well as display postures and sounds, especially in advertising behaviour. We also noted a specific ability of the birds to modulate their behaviour pattern towards either black grouse or capercaillie respectively (Porkert et al. 1997, cf. Hjorth 1970).

The presence of hybrids is a symptom of skewed sex ratio in capercaillie, in disfavour of males. The number of hybrids has increased in specific areas, first Middle Europe (Porkert 1990), and presently in Fennoscandia (Hjorth 1994 and pers. comm., Porkert 1996 and unpubl., Bakka 1996). Lack of capercaillie males both in small broods in S-Norway (Wegge 1980) and in rest-populations prior to their extinction in Middle Europe (Klaus et al. 1989, Porkert 1990, 1995b) has been recorded as well. The causes relates to interaction between the male capercaillie's morphophysiology and environmental factors. Male capercaillie chicks have a much faster growth rate and retarded flight ability (Kalske & Lindén 1988) during their first summer than female chicks, and are thus prone to higher physiological strain (Lindén 1981, Lindén et al. 1984) and higher vulnerability to predation (Kalske & Lindén 1988). Reduced habitat quality is the most likely factor causing such sex-biased growth strain today, and we can see the following possible causes:

1. Acid rain and wind-borne pollutants may have reduced the amount and species diversity of invertebrates available as food for capercaillie chicks (Fimreite 1977, Valeur 1977). Pollution caused vegetation changes in capercaillie habitats where the species later went extinct, especially in dwarf shrubs and grass layer (Porkert 1979, 1980, 1982, 1983, 1991a, b, 1995b, Klaus et al. 1989). The nutritional value of the main food plants are reduced in the polluted areas and the content of harmful substances (i. e. metals) increase (Porkert 1991b tab. 4, unpubl. data from the Czech Republic and Germany, cf. Klaus et al. 1985).

2. The quality of food plants may be reduced as a result of heavy competitive browsing by very dense ungulate (i. e. moose *Alces alces*, red deer *Cervus elaphus* and roe deer *Capreolus capreolus*) populations. Heavy browsing increase the plants' production of chemical anti-browsing agents, which in turn may have a negative effect on the reproduction of small game like grouse (cf. Selås 1997).

3. By browsing and trampling, dense ungulate populations may also degrade the food plants' (*Vaccinium* and *Filicales*) cover quality for capercaillie chicks as protection against predators and



Figs 2-5. 2 – wing-beat display of male hybrid; 3 – drumming flight of male hybrid; 4 – thin-necked upright display posture of male hybrid; 5 – male hybrid running towards a rival, tilting tail towards him.



Figs 6-9. 6 - male hybrid displaying close to a male black grouse without attacking him; 7 - male hybrid approaching female capercaillie prior to copulation; 8 - male hybrid begins mating like capercaillie; 9 - male capercaillie mating with females on "mating ground" in 1997, which in 1996 was occupied by a male hybrid (see text). Figs 2 to 8 Jan Porkert, Fig. 9 Arne Flor.

precipitation, especially prior to development of the chick thermoregulation mechanism (Müller 1982, Porkert 1982, 1983, Klaus et al. 1985, 1989).

4. Capercaillie habitats are regularly degraded by old forest logging and bog drainage, which cause habitat fragmentation with many negative effects (Klaus et al. 1989, Rolstad 1989 and others).

Under the lack of the male capercaillies, the mating behaviour of both black cock and capercaillie female (Höglund 1957, Hjorth 1994) favour hybridization. Unfortunately, we are short of information on the fertility of hybrids. Female hybrids are sterile, but some males may reproduce with females of the parent species (Höglund & Porkert 1989, cf. Collett 1906). Male hybrid chicks may have better survival options than male capercaillie chicks, due to slower growth rate during the first weeks after hatching (Höglund & Porkert 1989: Fig. 1). An intermediary diet of hybrids consisting of food components of both parent species (Porkert 1972, Pulliainen 1982), may also give this effect. This may however not counterbalance the hybrids' lower fertility. Females are in general more choosy than males (Hjorth 1970, Höglund & Porkert 1989, cf. Fig. 6 male black grouse mounting a stuffed female capercaillie). The choosiness of female has recently been demonstrated experimentally in flycatchers by Saetre et al. (1997a). In sympatric populations of two related species, female choice even select for divergence in male appearance between the species (Saetre et al. 1997b). However, among birds in general, about one out of ten species has been proved to hybridize with related species, Galliformes being one of the orders with the highest frequencies of hybridization (21.5% of all species hybridize, Grant & Grant 1992). Both capercaillie and black grouse may even produce hybrids with Phasianids (Gray 1958, cf. reference in Höglund & Porkert 1989, Klaus et al. 1989). Hybrids of some Darwin's finches in the Galapagos archipelago have even been proven better survivors than their mother species (Grant & Grant 1992). The presence of hybrids in degraded grouse habitats with deteriorated microclimatic conditions may be viewed as a parallel, and a basis for further studies of the survival abilities of "rakkelhons" hybrids and their backcross hybrid progeny in anthropogenetically disturbed habitats.

CONCLUSION

The behaviour of the "mother" species (capercaillie) dominates the display behaviour of hybrids. But individual variation and flexibility in the modulation of behaviour to suit different situations point to relatively low genetic fixation. Thus both comparison with the behaviour of hybrid F_1 -males resulting from male capercaillie \times female black grouse crosses, and further backcrossings would be most interesting (cf. i. e. sonogram of display songs from F_1 and F_2 hybrids raised in Boda Viltforskningsstation in Sweden, Höglund & Porkert 1989, described by Klaus et al. 1989, Fig. 26, and supposed F_2 - F_3 hybrids observed in nature or found in museum collections, Anon. 1883, Meyer 1887, Klaus et al. 1989, Porkert 1995a, Porkert et al. 1996).

Our study area in southern Norway with female capercaillies regularly inviting male hybrids for mating thus present a unique opportunity for field studies of the outcome of such crossings. By the use of radiotelemetric equipment, it should be possible to find potential nests or clutches with F_2 -hybrid offspring, and thus record the fitness value of capercaillie and black grouse hybridization. We also stress the need for systematic cross-breeding experiments with capercaillie and black grouse in captivity, to collect accurate data on the hybrids' and later backcrossed progeny's fertility, morphophysiology and genetics.

Acknowledgements

We thank Hans Chr. Pedersen for comments on a Swedish draft of this manuscript, and Jon Swenson for comments and correction of language on a earlier draft. We also thank Ingemar Hjorth for personal comments, comments

on the manuscript and information of Nyströms observations, Bjørn Bjerke for personal communications and Asbjørn Lie for observational contribution in 1997. We are deeply indebted to Svein Per Hardeberg and Kristian Hørte for practical support in the study areas.

REFERENCES

- ANONYMUS (Kronprinz Rudolf von Österreich) 1883: Neue Notizen über Tetrao medius. *Mitt. Ornithol. Ver. Wien* 7: 105–109.
- BAKKA D. 1996: Rackelhöonor ett dåligt tecken. *Jaktjournalen* 1996 (November): 50–52.
- BERGMAN S. 1940: En korsning mellan rackelhane och tjäderhöna. *Fauna och Flora* 35: 57–62.
- COLLETT R. 1906: Hybrids among Norwegian Birds, and their diagnoses. *Christiania Vidensk.-Selsk. Forhandl.* 1905(11): 1–26.
- COUTURIER M. & COUTURIER A. 1980: *Les coqs de bruyère*. Grenoble, 1529 pp.
- FIMREITE N. 1977: Sur nedbør og nedgang i norsk skogsfuglbestand. Foredrag fra Nordisk skogsfuglsymposium 1976. *Vilt rapport* 5: 82–91
- FLOR A. 1993a: Rackelhane parret seg med roy. *Fauna* 46: 196–197.
- FLOR A. 1993b: Biologisk sensasjon in Øvre Landvik. *Liv i Landvik* 2(5): 377–379.
- GRANT P. R. & GRANT B. R. 1992: Hybridization of birds species. *Science* 256: 193–197.
- GRAY A. P. 1958: Birds hybrids – a check list with bibliography. Fam. Tetraonidae. *Techn. Comm.* 13: 79–85.
- HJORTH I. 1970: Reproductive behaviour in Tetraonidae with Special Reference to Males. *Viltrevy* 7: 181–596.
- HJORTH I. 1994: *Tjädern. En skogsfågel*. Jönköping: Skogsstyrelsen, 182 pp.
- HÖGLUND N. H. 1957: [Instinctive activities in captive Swedish Tetraonidae in connection with mating]. *Viltrevy* 1: 225–232 (in Swedish).
- HÖGLUND N. H. & PORKERT J. 1989: Experimentelle Kreuzungen zwischen Auer- und Birkhuhn. (Tetrao urogallus et Tetrao tetrix). *Ztschr. Jagdwiss.* 35: 221–234.
- KALSKE A. & LINDÉN H. 1988: Sexual differences in flight ability of capercaillie chicks. *XI Nordic Congr. Game Res. Espoo, Finland. Abstr. P.* 35.
- KLAUS S., BOOCK W., GÖRNER M. & SEIBT E. 1985: Zur Ökologie des Auerhuhns in Thüringen. *Acta Ornithoecol.* Jena 1: 3–46.
- KLAUS S., ANDREEV A. V., BERGMANN H.-H., MÜLLER F., PORKERT J. & WIESNER J. 1989: *Die Auerhühner Tetrao urogallus und T. urogalloides. Neue Brehm-Bücherei* 86. 2. durchges. Aufl. Wittenberg Lutherstadt: A. Ziemsen Verlag, 280 pp.
- KLAUS S., BERGMANN H.-H., MARTI C., MÜLLER F., VITOVIC O. A. & WIESNER J. 1990: *Die Birkhühner Tetrao tetrix und T. mlokostewiczi. Die Neue Brehm-Bücherei* 397. Wittenberg Lutherstadt: A. Ziemsen Verlag, 280 pp.
- KOIVISTO I. 1965: Behaviour of the Black Grouse during the Spring Display. *Finnish Game Res.* 26: 1–60.
- KRUIT J. P. & HOGAN J. A. 1967: Social behaviour of the lek in Black Grouse. *Ardea* 55: 203–240.
- LINDÉN H. 1981: Growth rates and early energy requirements of captive juvenile capercaillie, Tetrao urogallus. *Finnish Game Res.* 39: 53–67.
- LINDÉN H., MILONOFF M. & WIKMAN M. 1984: Sexual differences in growth strategies of the capercaillie Tetrao urogallus. *Finnish Game Res.* 42: 29–35.
- MEYER A. B. 1887: *Unser Auer-, Rackel- und Birkwild und seine Abarten*. Wien: A. W. Kunast. XII+95 pp., Atlas 17 Tafeln
- MÜLLER F. 1982: Causes de regression du grand tetras en Europe Centrale et les mesures conservatoires à envisager. Pp.: 90–111. In: *Actes Coll. Int. Grand Tetras Tetrao urogallus major*. Colmar, 286 pp.
- NYSTRÖM H. 1990: *Vättelefall och Lärjeån*. Göteborg: Tre Böcker, 218 pp.
- PORKERT J. 1972: Zum Gritwechsel bei unseren Waldhühnern (Tetraonidae). *Věst. Čs. Společ. Zool.* 36: 134–159.
- PORKERT J. 1976: Methoden zur Untersuchung der Fortpflanzungsbiologie bedrohter Tetraoniden-Populationen (Aves: Galliformes). *Věst. Čs. Společ. Zool.* 40: 41–52.
- PORKERT J. 1979: The influence of human factors on Tetraonid Populations in Czechoslovakia. Pp.: 74–82. In: T. W. I. LOVEL (ed.): *Woodland Grouse. Proc. Int. Symp. Grouse I*. WPA Suffolk, 178 pp.
- PORKERT J. 1980: Vergrasung des Waldbodens als Birkwildproblem. *Beih. Veröff. Naturschutz Landschaftspflege Baden-Württemberg* 16: 75–95.
- PORKERT J. 1982: Pas de chance de survie du Grands Tetras dans les Sudetes Orientales. Pp.: 120–136. In: *Actes Coll. Int. Grand Tetras Tetrao urogallus major*. Colmar, 286 pp.
- PORKERT J. 1983: Einige Faktoren, die die Überlebenschancen der Tetraoniden in Ostsudeten beeinflussen. *Proc. XVI IUGB Congr.* Pp.: 668–678.
- PORKERT J. 1990: Zu Bastardierungen in den Anstiegs- und Aussterbensphasen einiger mitteleuropäischen Populationen des Auerhuhns Tetrao urogallus (Tetraonidae, Aves). *Acta Soc. Zool. Bohemoslov.* 54: 56–68.

- PORKERT J. 1991a: Hoarfrost deposits as a factor contributing to the extinction of tetraonids in the eastern Sudetes. In: JENKINS D. (ed.): Proc. Int. Symp. Grouse 5. *Ornis Scand.* **22**: 292–293.
- PORKERT J. 1991b: Nebelfrost als das Aussterben von Tetraoniden fördernder Faktor in den Ostsudeten. *Acta Ornithoecol. Jena* **2**: 195–209.
- PORKERT J. 1995a: [Hybrids between Capercaillie (Tetrao urogallus) and Black Grouse (Tetrao tetrix) and their characteristics.]. *Fauna* **48**: 52–61 (in Norwegian).
- PORKERT J. 1995b: Nebelfrostdeposition, Heidelbeerrückgang, Auftreten von Rackelhühnern-Begleiterscheinungen des Aussterbens von Auerhuhn (Tetrao urogallus) und Birkhuhn (Tetrao tetrix) im Orlické Hory (Adlergebirge), Tschechien. *Naturschutzreport* **10**: 173–182.
- PORKERT J. 1996: Dør storfuglen ut i Øvre Landvik? *Liv i Landvik* **3**: 261–262.
- PORKERT J., LIFJELD J. T. & TORNBORG R. 1996: Backcrossings of Tetrao hybrids (T. tetrix male × T. urogallus female) with their parent species: a descriptions of female offspring based on museum skins. *Aquilo, Ser. Zool.* **29**: 33–41.
- PORKERT J., SOLHEIM R. & FLOR A. 1997: Behaviour of hybrid male Tetrao tetrix × T. urogallus on black grouse leks. *Wildlife Biol.* **3**: 169–176.
- PULLIAINEN E. 1982: Food selection in the tetraonid hybrids Lyrurus tetrix × Tetrao urogallus, Lyrurus tetrix × Lagopus lagopus and Tetrao urogallus × Lagopus lagopus. *Ornis Fennica* **59**: 170–174.
- ROLSTAD J. 1989: *Habitat and range use of capercaillie Tetrao urogallus L. in southcentral Scandinavian boreal forests, with special reference to the influence of modern forestry.* Dr. Agric. Thesis Ås-NLH.
- SELÅS V. 1997: Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants: the mast depression hypothesis. *Oikos* **80**: 257–268.
- SAETRE G.-P., KRÁL M. & BUREŠ S. 1997a: Differential species recognition abilities of males and females in a flycatchers hybrid zone. *J. Avian Biol.* **28** : 259–263.
- SAETRE G.-P., MOUM T., BUREŠ S., KRÁL M., ADAMJAN M. & MORENO J. 1997b: A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* **387**: 589–592.
- VALEUR P. 1977: Nedgang i skogfuglbestanden i relasjon til sur nedbør. Foredrag fra Nordisk skogsfuglsymposium 1976. *Viltrapport* **5**: 92.
- VHHT E. 1987: [*The Black Grouse in Estonia*]. Tallinn: Valgus, 152 pp (in Estonian).
- WEGGE P. 1980: Distorted sex ratio among small broods in a declining Capercaillie population. *Ornis Scand.* **11**: 106–109.