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Behaviour of hybrid male *Tetrao tetrix* ♂ × *T. urogallus* ♀ on black grouse leks

Jan Porkert, Roar Solheim & Arne Flor

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Crosses between male black grouse *Tetrao tetrix* and female capercaillie *T. urogallus* are the most common grouse hybrids. Some male hybrids (F₁-generation) may be fertile and produce offspring (F₂-generation) with females of capercaillie and, rarely, black grouse. Specimens and descriptions of lek behaviour are also available for probable F₃- and F_{3,3}-hybrids. Three and two male F₁ hybrids were documented to display simultaneously on a black grouse lek in Norway (1993-1997), and solitarily displaying hybrids were documented on black grouse leks in the Czech Republic (1960-64), Sweden (1991-93) and Norway (1992). Mating of hybrid males with female capercaillie was observed in 1992 and 1994. The lekking behaviour of the hybrids and their attitudes towards other tetraonids are described.

Key words: black grouse × capercaillie hybrids, lekking behaviour, *Tetrao tetrix*, *Tetrao urogallus*

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Hybrids between male black grouse *Tetrao tetrix* and female capercaillie *T. urogallus* are the most common grouse hybrids, termed 'rakkelhane' in Norwegian. Some male hybrids (F₁-generation) may be fertile and produce offspring (F₂-generation) with females of both capercaillie and black grouse. Skin material and descriptions of lekking behaviour also exist for probable F₃- and F_{3,3}-hybrids. Successively increased fertility is suspected through such backcrossings (Bergman 1940, Höglund & Porkert 1989, Porkert 1995a, Porkert, Lifjeld & Tornberg 1996).

Male F₁-hybrids usually occur solitarily on black grouse leks, and act aggressively towards male black grouse. We have found two reports of collectively displaying hybrids. Crown Prince Rudolf of Austria (Anon. 1883) mentioned four hybrids displaying on a capercaillie lek in northeastern Bohemia, of which two supposed F₃-hybrids were shot on the same day (Meyer 1887, Klaus, Andreev, Bergmann, Müller, Porkert & Wiesner 1989, Porkert 1995a). Viht (1987)

reported three hybrids displaying in 1971 and 1972 on a black grouse lek with approximately 20 male black grouse in Estonia. In this paper we describe the lekking behaviour of hybrids based on our own observations of solitarily (Czech Republic 1960-64, Sweden 1991-93, South-Norway 1992) and collectively (South-Norway 1993-95) displaying 'rakkelhane'.

Methods

Hybrids displaying on the black grouse lek at Øvre Landvik was first documented by Arne Flor in 1992. Jan Porkert and Roar Solheim took part in the observations from 1994 and 1995, respectively. Observations were made from blinds close to the lek centres, and the birds' behaviour was documented by photography and video taping. Descriptions follow Hjorth (1970). Figure drawings are made by Roar Solheim,

based on photos by Jan Porkert and video recordings by Arne Flor.

Results

During spring 1992, one hybrid was present on the black grouse lek in Øvre Landvik, Southern Norway (Fig. 1), whereas during 1993 and 1994 there were three hybrids on this lek together with three male black grouse that displayed in parts of the territories of the hybrids. In 1995 and 1996, the lek contained two 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. Observations from this capercaillie lek are not included in the present paper. Observation days, observed behaviour and interactions among different birds are given in Table 1. Below we describe the patterns of behaviour observed in hybrid males.

Announcing behaviour

'Announcing with upright and standing on ground without moving forward', similar to black grouse

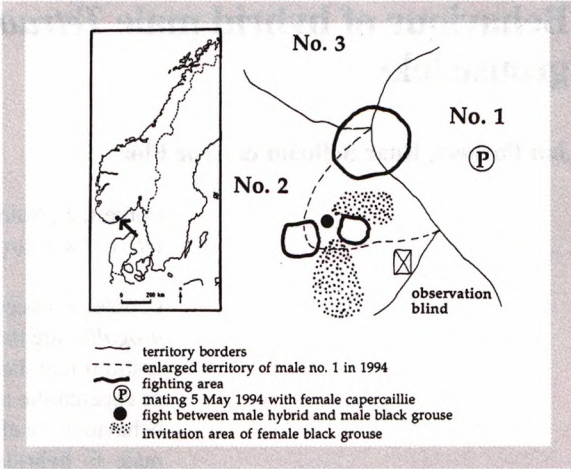


Figure 1. Location of the black grouse lek in Øvre Landvik, South Norway, with the territories of three hybrids in 1993 and 1994.

(Hjorth 1970: fig. 78), is the weakest form of announcing (Fig. 2).

'Announcing with "drumming flight"' similar to male capercaillie (Hjorth 1970: Fig. 58), mostly straight forward about 2-5 m, height 1-1.5 m (Fig. 3). If a rival or female is present, the male will land fac-

Table 1. Observation days and periods on the black grouse lek at Øvre Landvik, with numbers of hybrids and female capercaillies and black grouse being present and indications of the behaviour of hybrid 'rakkelhaner' towards conspecifics, female grouse, and male black grouse.

Year/ Observation period	No of days	No of hybrids	No of ♀ capercaillie	No of copulations	No of ♀ black grouse	No of copulations	No of days with fights with ♂ conspecifics	No of days with aggression towards ♂ black grouse	Notes	Observer and no of 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 ⁱⁱ : 5.5 mostly quiet in territory	AF 4 JP 6 JP 3
21-23.5	3	3-1	0		0		0	0	No activity 1.10	JP 2
30.9	1	2	0		0		0	0		
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 ⁱⁱⁱ	0	?	1+2 ⁱⁱⁱ	ⁱ : 24.4, ⁱⁱ : 25.4, ⁱⁱⁱ : 26.4; heard ⁱⁱⁱ : 1.5; solicitation	AF 6 RS 6
4-7.5	4	1-2	0		0		0	0	Low activity	JP4
10.5	1	2	0		0		0	0	8.5: rain, no birds	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 : 4.5, solicitation, fight ⁱⁱ : 5 and 7.5 flew over the lek; 6.5 solicitation	JP 6

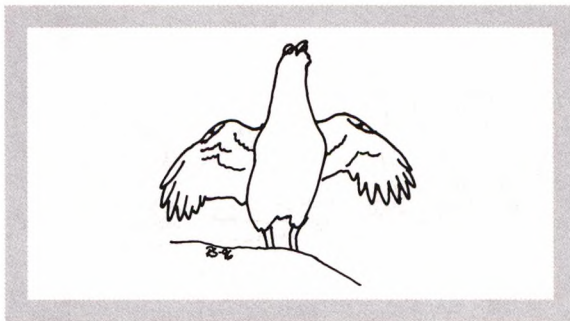


Figure 2. Wing-beat display of male hybrid.

ing it. Drumming flight may be reduced to a short run similar to that of black grouse. Announcing may lack vocal sounds, as in capercaillie, most often during drumming flights similar to those of capercaillie, or vocal announcing may vary from a short part of the hybrid display sound to a coarser monosyllabic sound resembling the 'tsjui' sound of black grouse. Hybrids may thus alternate between the drumming flight of either capercaillie or black grouse at landing and between the accompanying announcement sounds.

Both forms of announcement serve to mark the male hybrid's territory. The two forms occur during both morning and evening displays, but most frequently during morning displays.

'Thin-necked upright' (Fig. 4). This behaviour is commonly displayed on the ground and in trees to demonstrate the dominance of the territory holder (Hjorth 1970). The hybrid stands still or slowly moves in a posture very similar to the capercaillie's "thin-necked upright posture" (Hjorth 1970: Fig. 59). While emitting the display sound, the neck is held almost vertically ($<20^\circ$ difference from vertical), but the head does not vibrate during the last phase as in capercaillie (Hjorth 1970: Fig. 60). Only convulsive head movements up and down at an angle of approx-

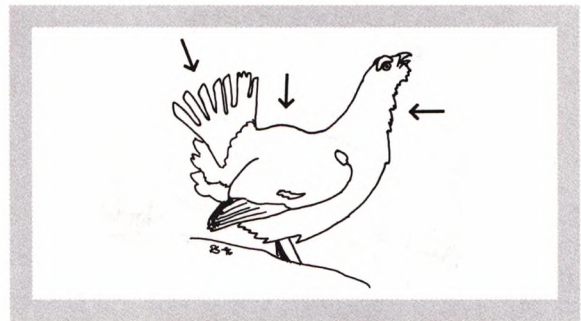


Figure 4. Thin-necked upright display posture of male hybrid. The arrows indicate characters intermediate between black grouse and capercaillie, typical of hybrid.

imately $5-10^\circ$ may be used as a hybrid character (the head of male black grouse is held in the same angle during rookooing call). The bill is pointing upwards in an angle of approximately $30-40^\circ$ from vertical, and remains open during most of the display sound sequence. As in the capercaillie, there is no erection of neck feathers. While emitting the display sound, a 'wave' of slightly erected ventral neck feathers can be seen at the larynx. Tail feathers are usually erected $<180^\circ$, and raised to a maximum of 90° above horizontal, occasionally showing a slight gap between feathers (see Fig. 4). Back and rump feathers are slightly erected, showing an intermediary character between black grouse (strong erection of these feathers) and capercaillie (no erection) (Hjorth 1970: Fig. 59, 81). While displaying in trees, the neck is held in a more forward position, and the tail is spread less if erected (up to approximately 45° above horizontal, Fig. 5).

The display sound is an individually varying, recurring "crrrrs"-sound, which mostly reaches 1-2 KHz, but which may reach approximately 4 KHz (Klaus et al. 1989: Fig. 26).

'Upright cum wing-dragging, singing and tail-tilt-

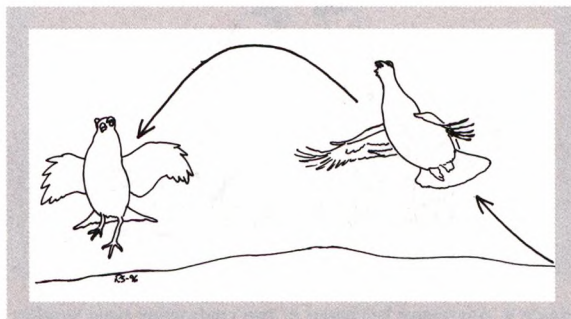


Figure 3. Drumming flight of male hybrid.



Figure 5. Male hybrid with thin-necked upright posture while displaying in a tree top.

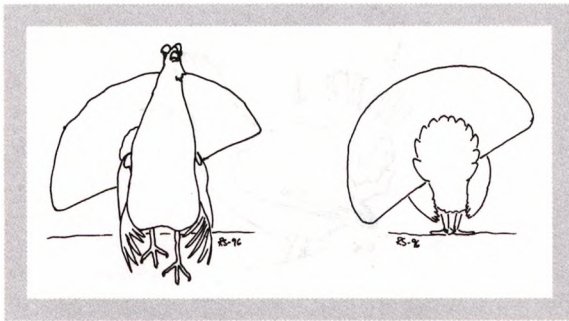


Figure 6. Male hybrid running towards female or displaying close to a rival, tilting tail towards the intended partner/rival.

ing' (Fig. 6) is similar to that in capercaillie (Hjorth 1970: Fig. 63). The tail is fully fanned ($\geq 180^\circ$), bends $20\text{--}30^\circ$ forward from vertical towards the back, and the primaries are spread out and touch the ground. The tail is tilted $30\text{--}40^\circ$ sideways towards the female or rival, preparing for either copulation or confrontation. The sideways tilting is more pronounced than in both capercaillie and black grouse.

Aggressive behaviour

'Head and neck "bowing"' (Fig. 7), with a modulated display sound is the weakest form of aggressive behaviour, resembling "wide-necked attitudes cum belching cantus" in capercaillie (Hjorth 1970: Fig. 64). This aggressive attitude marks the territory and scares away rivals, and is displayed towards both conspecific hybrids or male black grouse on the ground and in trees, both during morning and evening.

'Fighting with wing beats and/or pecking' between hybrids is similar to capercaillie behaviour (Hjorth 1970: Fig. 65, 67), and is initiated and occasionally terminated with deep bowing by both rivals (Fig. 8). The birds often try to start beak pecking (Fig. 9) or

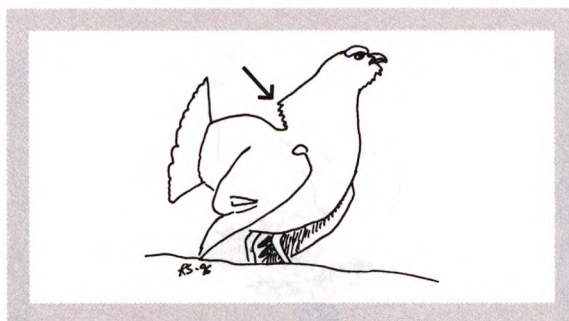


Figure 7. Male hybrid marking its territory by wide-necked attitude. The arrow indicates the erected neck feathers, similar to capercaillie,

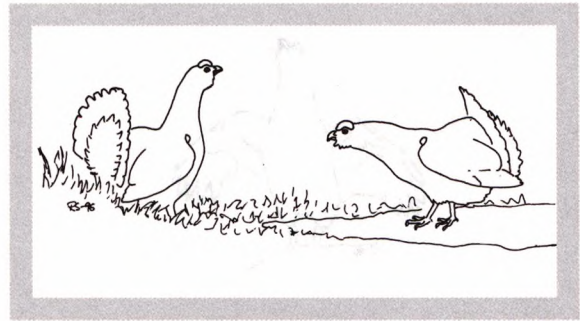


Figure 8. Aggressive behaviour of two confronting male hybrids. Note that neck bowing is displayed by the bird standing on bare rock, the most attractive part of the territory.

wing-beat fighting (Fig. 10). Beak pecking is directed towards the head or chest of the rival, and not intentionally towards the red eye spots as in black grouse. This behaviour is mostly observed between hybrids themselves. Male black grouse avoid confrontations by fleeing. Only twice (1 May 1995 and 4 May 1996) was a short wing-beat fight observed between a male hybrid and a male black grouse, probably provoked by the presence of three soliciting female black grouse.

Copulation behaviour

Matings with female capercaillies were observed on 26 April 1992 (AF) and 5 May 1994 (JP). In 1992, a single male hybrid mated several times with two female capercaillies (Flor 1993a,b), of which two were documented on video film. Apparently, some mounting attempts failed. In 1994, one female capercaillie was observed on the lek, and mating was seen only once. Female capercaillies showed no interest in male black grouse. They invited the dominant hybrid to mate immediately after arriving in his territorial centre (Fig. 11).

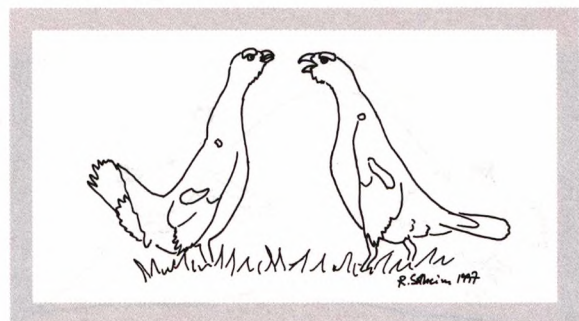


Figure 9. Aggressive behaviour of two confronting male hybrids; beak pecking.

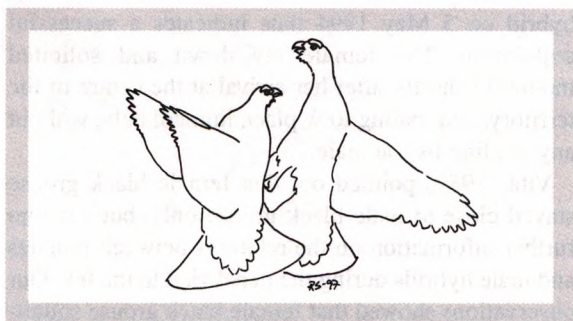


Figure 10. Aggressive behaviour of two confronting male hybrids; wing beat fighting and kicking.

In 1992, a male hybrid circled the female capercaillie before mounting, a behaviour similar to that of male capercaillie. He mounted slantingly from behind, grabbing the female's neck with the beak (Figs. 12 and 13). During the first video-documented mating between a hybrid and a female capercaillie, the male made two wingbeats at the start and one at the end of the mating sequence, without losing his grip with the beak. On 5 May 1994 a male mounted slantingly from behind (right side) without any pre-circling (see Fig. 11), barely 20 seconds after the beginning of the female's first invitation to mate. Mating started as in the capercaillie, without wingbeats, but at the end the hybrid made two wingbeats as he let go of the female's neck (for photos, see Porkert 1996). The copulation lasted approximately 4 seconds. Thereafter the female shook its body, mended its feathers for approximately 20 seconds and flew away.

Our observations show that hybrids may either initiate mounting like a male capercaillie (Fig. 12, Höglund 1957, Couturier & Couturier 1980: pl. LX, Klaus et al. 1989: Fig. 39) without any wingbeats and end like a male black grouse (Fig. 13, Hjorth 1970:

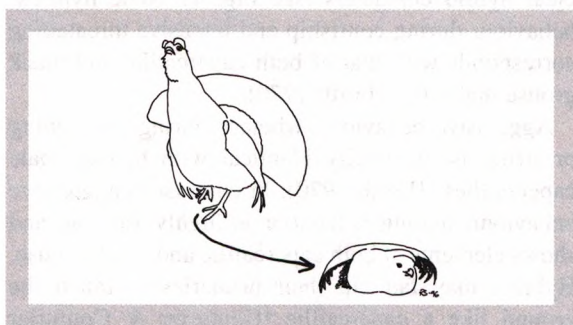


Figure 11. Male hybrid approaching female capercaillie from behind, shortly before mounting.

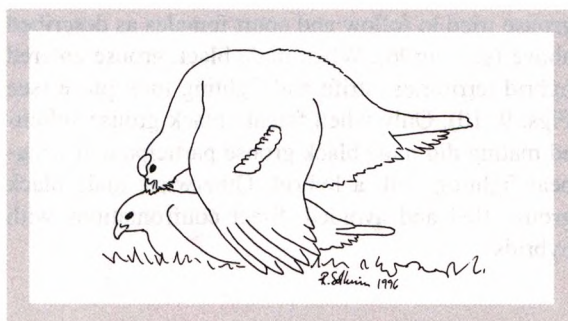


Figure 12. Male hybrid mating with female capercaillie. Note downwards position of wings, as in capercaillie.

Fig. 85, Klaus, Bergmann, Marti, Müller, Vitovic & Wiesner 1990: Fig. 28, 29) with a few wingbeats, or make a few wingbeats at the beginning of the mounting.

On 4 May 1995 and 6 May 1996 female black grouse were observed soliciting mating. The solicitations were probably also meant for a male black grouse, which was circling a displaying hybrid at a distance of 3-5 m. However, each time the hybrid was close enough for mounting, the female rose and went away. The solicitation behaviour did not take place at the locations of the lek where female capercaillies had solicited mating.

In contrast to solitarily displaying hybrids, collectively displaying hybrids at Øvre Landvik were much more tolerant towards male black grouse. A two-level hierarchy developed on this lek. Male hybrids had fixed territories according to their individual status (see Fig. 1). Male black grouse displayed close to the hybrids as long as they stayed on the secondary parts of the lek, in trees, or in thick heather vegetation, not moving on to bare rock in the hybrids' territories. Only when female grouse arrived on the lek did this hierarchy break up, and both male hybrids and black

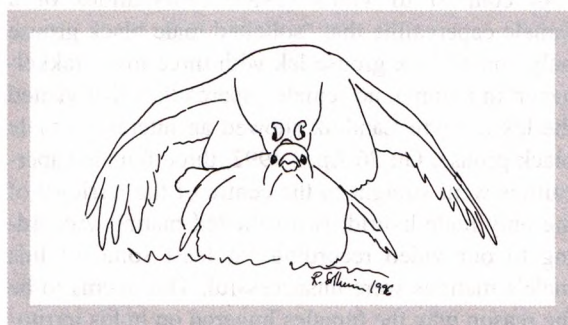


Figure 13. Mating phase with wing beats, as in black grouse.

grouse tried to follow and court females as described above (see Fig. 6). When male black grouse entered hybrid territories, strife and fighting took place (see Figs. 9, 10). Only when female black grouse solicited mating did male black grouse participate in wing-beat fighting with a hybrid. Otherwise, male black grouse fled and avoided direct confrontations with hybrids.

Discussion

Although the hybrid 'rakkelhane' was described as early as 1744 (Rutenschiöld in Meyer 1887), and even though there are many reports in the literature of hybrids at both black grouse and capercaillie leks, hybrid behaviour has been described only cursorily. This contrasts with 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 hybrids according to the terminology used by Hjorth (1970).

At the end of the 1950s, as male capercaillies gradually disappeared from the Adlergebirge in the Czech Republic due to habitat degradation caused by pollution and modern forestry (Porkert 1979, 1980, 1982, 1991b) and eventually died out, male black grouse became more aggressive and started displaying solitarily (Porkert 1976). During the so-called 'rakkel'-phase (1959-64) of the grouse extinction in the Adlergebirge (Porkert 1990, 1991a,b, 1995b), male hybrid aggression excluded any black grouse display on or close to the lek. Similarly, aggressive behaviour was observed on a black grouse lek with one male hybrid at the Grimsö Research Station in south-central Sweden. After this male turned up on the lek, female black grouse stayed away.

In contrast to Viht's (1987) observations of a female capercaillie that "solicited male black grouse only" on a black grouse lek with three male 'rakkelhaner' in Estonia, no female capercaillies that visited the lek at Øvre Landvik showed an interest in male black grouse. On 26 April 1992, three female capercaillies went straight to the centre of the territory of the only male hybrid; two solicited mating. According to our video recordings at least some of this male's matings were unsuccessful. This seems to be the reason why the females lingered on in his territory, soliciting mating. A female capercaillie's brief visit in the territory centre of the old, dominant male

hybrid on 5 May 1994 thus indicates a successful copulation. The female lay down and solicited mounting shortly after her arrival at the centre of the territory, and mating took place immediately, without any circling by the male.

Viht (1987) pointed out that female black grouse stayed close to male black grouse only, but gave no further information on the relations between females and male hybrids during the hens' visit to the lek. Our observations showed that female black grouse solicited only male black grouse for mounting. However, due to the presence of male hybrids, male black grouse were deterred from mating. All female black grouse stopped soliciting shortly after a male hybrid came too close. This suggests that copulation between a male hybrid and a female black grouse is unlikely, unless a highly receptive female turns up on a hybrid's lek without male black grouse. Thus our observations may explain why more F₂-hybrid skins of 'rakkel' male × capercaillie female than 'rakkel' male × black grouse female were found in museum collections (Porkert et al. 1996).

As male hybrids show variation in character, display sounds, and probably fertility (unpubl. data), there is also individual variation in behaviour. We recognised different 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 and vocalisation. We also noted an ability for birds to modulate their behaviour pattern towards either black grouse or capercaillie (Hjorth 1970). This modulation is most pronounced during announcing (see Figs. 2-3). During thin-necked upright displays, the posture of the hybrid mostly resembles that of a male capercaillie. However, by the raising of feathers on the back, neck and the tail feathers intermediate between the behaviour of black grouse and capercaillie (Hjorth 1970), hybrids show clear hybrid characters (see Fig. 4). Male hybrids' behaviour during courtship and intensive threatening corresponds with that of both capercaillie and black grouse males (cf. Hjorth 1970).

Aggressive behaviour, whether during threatening or strife, is practically identical with that of male capercaillies (Hjorth 1970). In contrast to aggressive behaviour, mating behaviour is highly variable and shows elements of both capercaillie and black grouse. Hybrids may fan out their primaries to touch the ground like a capercaillie (Couturier & Couturier 1980: pl. II, Klaus et al. 1989: Fig. 39), most often at the start of mating, or they may make a few wing

beats at the end of mating as a remnant of the male black grouse wing flutter (Hjorth 1970: Fig. 85, Klaus et al. 1990: Fig. 28, 29).

In 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 points to a relatively low heritability fixation. A comparison with behaviour of hybrid F_1 -males from male capercaillie \times female black grouse would be most interesting. Due to the large size differences between the sexes such hybrids are, however, unlikely under natural conditions, although they have been produced in captivity (Höglund & Porkert 1989). Unfortunately, the only such male from captivity was injured as a chick and did not show any display behaviour, although the bird reached an age of two years and eight months. Also, behaviour of F_2 -hybrids ((male black grouse \times female capercaillie) \times female capercaillie) would shed light on the heritability of such characters. Sonograms from such hybrids are described by Klaus et al. (1989: Fig. 26), and short notes even describe supposed F_2 - F_{3-5} hybrids observed in nature (Anon. 1883, Klaus et al. 1989, Porkert 1995a).

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