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S17-1 Ethological and acoustical characters of the Chinese grouse (*Bonasa sewerzowi*), compared with sibling hazel grouse (*B. bonasia*) and ruffed grouse (*B. umbellus*)

Wolfgang SCHERZINGER[1], Siegfried KLAUS[2], SUN Yue-Hua[3*], FANG Yun[3]
1. Nationalpark Bayerischer Wald, Guntherstrasse 8, D-94568 St. Oswald, Germany; drscherzinger@gmx.de
2. Thüringer Landesanstalt für Umwelt, Prüssingstraße 25, D-07745 Jena, Germany; s.klaus@tlujena.thueringen.de
3. Institute of Zoology, China Academy of Sciences, Beijing 100080, China; *sunyuehua@sina.com

Abstract Woodland grouse of the genus *Bonasa* occur allopatrically in circum-polar temperate and boreal forests. An interspecific comparison of the size and pattern of eggs, the downy feathers of pulli and other morphological characters in the three species suggests convergence in character sets. Yet species-specific differentiation is evident in the color and number of tail feathers, in signals of territorial advertisement, and in investment for nest-site preparation, mate guarding and caring for the brood. When ranking specific characters of *Bonasa* species, the hazel grouse (*B. bonasia*) shows the richest diversity of vocalization, while the range-restricted Chinese grouse (*B. sewerzowi*) appears to be the least varied. Reconstruction of the speciation of woodland grouse based on morphology, ethology and mitochondrial DNA analysis indicates that the Chinese grouse seems to represent an archetypal form, not only in the genus *Bonasa* but for all tetraonids worldwide.

Key words *Bonasa*, Morphology, Behavior, Acoustical characters, Evolution

1 Introduction

The subfamily Tetraoninae is a well-defined group of Galliformes, which, restricted to the northern hemisphere, dwells mostly in forests and tundra and also, in the Nearctic, on open steppes. In this subfamily, the circumpolar genus *Bonasa* comprises three allopatric species: (1) the hazel grouse (*Bonasa bonasia*) which ranges widely across north Eurasia, (2) the ruffed grouse (*Bonasa umbellus*) which occurs over vast areas of northern North America, and (3) the Chinese grouse (*Bonasa sewerzowi*) which is anomalously confined to small pockets in east Asia, well isolated in the small forest belt adjacent to the Tibetan plateau. The great conformity of their ecological niches — clearings with young successional stands of forest of characteristic pioneer species — has resulted in a number of convergent adaptations in body size, cryptic plumage and locomotor specializations. Our intra-specific comparisons also reveal divergent species-specific differences which, in their variation, indicate pathways of radiation within the genus *Bonasa* and perhaps even tetraonids in general.

2 Materials and methods

Extensive field studies were carried out on the three species as follows:

Hazel grouse: alpine areas, Austria 1968–1980 and 1990–2002; Bavarian Forest National Park, Germany 1972–2000; Bialowieza National Park, Poland 1974–1975; Bohemian Forest, Czech Republic 1980–2002; Slovakian Paradise National Park, Slovakia 1984–1985; St. Petersburg, Russia 1982; Magadan, East-Siberia 1998; Changbai Mts, China 1992–1993.

Ruffed grouse: Duluth, Minnesota, USA 1986; Smithers, British Columbia, Canada 1986; Northern Cascades, Washington, USA 2001.

Chinese grouse: Lianhua Shan, Gansu Province, China 1994–2002; Jiuzhaigou, Sichuan Province, China 1997.

Detailed information about geographical and ecological conditions of the study areas is published in Bergmann et al. (1996), Klaus et al. (1996) and Sun et al. (2003). From the field program we compiled a database of observations and characters of the three species using the same protocols for observing, sound-recording and filming aspects of behavior, voice, and site features for interpreting the context, meaning and function of visual and acoustical signals. In addition, 2–3 pairs of hazel and ruffed grouse were kept in captivity over several years for more detailed observations of courtship, reproduction and chick-caring, as well as for tracking circadian rhythms.

3 Results

Acoustic signals for territorial advertisement are conspicuous, carry over great distances and are strikingly different between species. The hazel grouse utters a unique, extremely high-pitched “spearing” cantus (Fig. 1a); and the

Chinese grouse gives a whirring, bi-syllabic flutter-jump (Fig. 1b). Such signals reach their highest level of complexity in the ruffed grouse, which also gives an extraordinary wing-drumming that produces a series of low-pitched, thumping blows, accelerating to a quick whirr (Fig. 1c; also Bump et al., 1947; Gullion and Martinson, 1984; Hjorth, 1970). Furthermore, the ruffed grouse utters a broadly differentiated range of instrumental sounds that resemble rasping, slapping, flapping, clapping with wings against body or feet, stamping with feet or pecking the ground, all audible only within a short distance (Table 1; Scherzinger in Bergmann et al., 1996).

Signals used in short-distance communication in courtship or agonistic context are, in contrast, broadly similar among all species. During "offensive-run" display behavior, hazel males utter a specific "offensive-whistle" whereas male Chinese grouse sing a crumpling "offensive-cantus" with a constant and distinct rhythm. In "imposing" behavior against both rivals and females, males of all species fan the tail feathers conspicuously, spread the lowered wings moderately, and enlarge the body, fluffing ruffled plumage particularly on the neck.

Neck ruffling is extraordinarily specialized in the Ruffed Grouse, its prolonged, contrastingly colored neck feathers forming striking ruff around the head when erected. The effect of this signal is not only visually intensified by demonstrative head-twisting, but also acoustically stressed by a strange "wheezing-cantus", which resembles a starting locomotive. The twisting and wheezing then accelerates rythmically to culminate in the "rush", a powerful jump with grinding wing-tips and a long hissing note (Hjorth, 1970; Scherzinger in Bergmann et al., 1996). In all species, the "imposing" display is expressed maximally in pre-copulatory behavior, when the male struts in a "circular walk" around the female, dragging its wings on the ground. In both palearctic species, an "imposing warble" accompanies this excitement-generating behavior.

As environmental pressure may markedly affect selection in long-distance signals, vocalizations used in short-distance communication, in a non-agonistic context, are more appropriate for inter-specific comparisons of genetic relationship. The "whining" of abandoned chicks, for example, sounds similar in all three species, whereas their "moaning" notes become intensified by lining in a scale-like row. In this situation, chicks of Chinese grouse climb a bush up to 1.5 m high, as their "crying" from this elevated position may carry further. Because of high predator pressure on all small species of grouse, alarm calls are of high importance, especially at times of mating when pairs are in constant contact. Common to all three species is a rattling "twitter", a warbling "brurr", a shrill "craiy" or "crirr", and a soft groaning "serial warning". The staccato "cackle" was observed in only two species.

Although *Bonasa* species have only weakly differentiated syringes (Potapov, 1985), their vocal inventory is high in diversity. The hazel grouse is surprisingly endowed with 26 calls, and the Chinese grouse comparatively poor and simple; only 14 calls have been recorded, although a number of low-pitched sounds have still to be elucidated (Table 2).

4 Discussion

Among the three species of *Bonasa*, the Chinese grouse is the least complex in its vocalizations and behavior. It is usually supposed, when analyzing phylogenetic trees, that simpler specific characters are "older", or rather "primitive", and more complex characters "younger". The question then is: does the Chinese grouse resemble the ancestral form more closely, having conserved archaic characters during longtime isolation, or has its behavioral reper-

Table 1 Comparison of instrumental signals within the genus *Bonasa*

Characters	Chinese grouse *B. sewerzowi*	Hazel grouse *B. bonasia*	Ruffed grouse *B. umbellus*	Remarks
Flutter jump	■	■	■	
Wing dragging (in circular walk)	■	■	■	
Territorial display flight	■	■	▒	
Wing grinding (in rush)	?	■	■	
Wing slapping		■	■	
Wing clapping		■	■	
Foot stamping		▒	■	
Ground pecking (aggressive)		?	■	
Wing rasping (in strutting walk)			■	species specific
Wing drumming			■	species specific
Total = 10 signals	**3**	**6(7)**	**9(10)**	

Dark blocs = present and obligatory, pale blocs = present and facultative, and white blocs = absent. In all three species, advertising behavior is accompanied by non-vocal sounds, with greatest diversity in the ruffed grouse for short-distance communication.

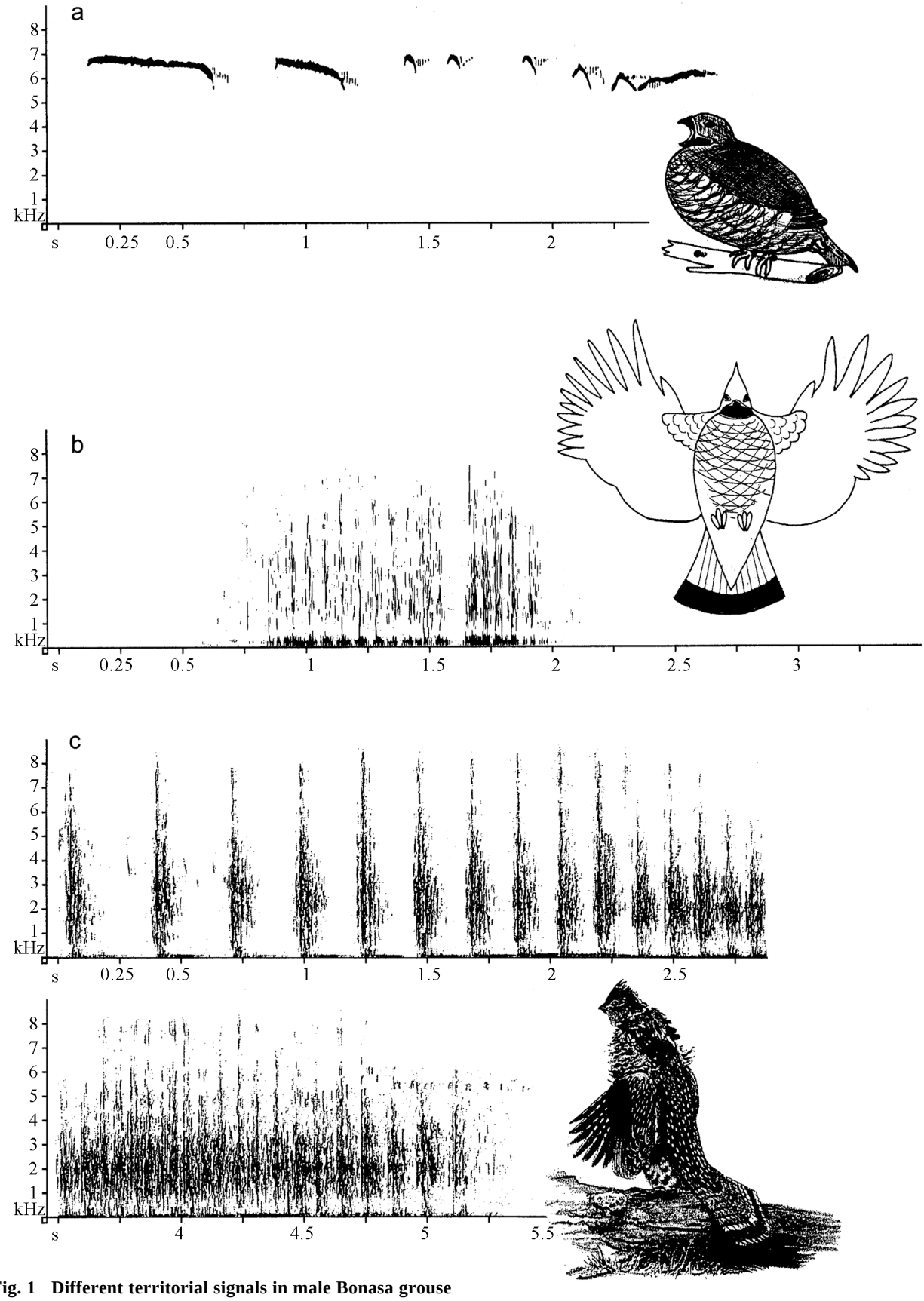

Fig. 1 Different territorial signals in male Bonasa grouse

(a) territory-marking "song" of the hazel grouse, a high-pitched whistle (tape recording of captive male, Germany); (b) primary advertising "flutter jump" signal of the Chinese grouse, typically disyllabic because of separate starting and landing phases (tape recording, from Gansu Province, China); (c) specialized territorial "wing-drumming" in the ruffed grouse, with thumping blows in a typical accelerating rhythm (tape recording of captive male, Germany).

Table 2 Inventory of vocalizations within the genus *Bonasa*

Characters	Chinese grouse *B. sewerzowi*	Hazel grouse *B. bonasia*	Ruffed grouse *B. umbellus*	Remarks
Adult grouse				
Simple contact call	■	■	■	
Intense contact call	■	■	■	
Scale	■	■	■	
Brooding note	■	■	■	
Serial warning	■	■	■	
Rattling twitter-alarm	■	■	■	
"Brurr"-alarm	■	■	■	
"Crraiy"-alarm / "crirr"-alarm	■	■	■	
Imposing warble	■	■		
Advertisement call (cock)		■	■	
Squeal (nest-site demonstration)		■	■	
Nesting note (egg laying)	?	■	■	
Chicken guiding note		■	■	
Cackle (warning)		■	■	
Hiss	?	■	■	
Offensive cantus ("crumpling")	■			species specific
Offensive whistle		■	?	spec. specific ?
"Peeyu" drawling alarm		■		spec. specific ?
Hen specific call		■		species specific
Territorial cantus ("spearing")		■		species specific
Cheeping (nest-site demonstration)		■		species specific
Serial "tsipp"-note (nest-demonstr.)		■		species specific
Fear twitter		■		spec. specific ?
Buzzing (in "follow up")			■	species specific
Wheezing cantus ("locomotive")			■	species specific
Whizzing sound (warning)			■	species specific
Groaning (warning ?)	?		■	spec. specific ?
Grouse chick				
Simple contact-call	■	■	■	
Intense contact-call	■	■	■	
Moaning / scale	■	■	■	
Fear-call	■			
Whining / whisper		■		spec. specific ?
Total = 32 calls	**14**	**26**	**21**	

Dark blocs= present, white blocs = absent. Basic utterances and chick calls are strikingly alike in all species, as are the repertoires of vocalization in hazel and ruffed grouse. The hazel grouse is the most diverse in vocal signals, and the Chinese grouse least.

toire become impoverished secondarily due to environmental pressures?

Recent reconstruction of *Bonasa* phylogeny by cytochrome-*b* sequences from the mitochondrial genome (Lucchini et al., 2001; Baba et al., 2002) confirm that *Bonasa* is monophyletic, that the ruffed grouse branched off very early, and that hazel and Chinese grouse diverged later, probably within the Pleistocene. This sequence and its timing seems paradoxical in the historical context of grouse evolution.

The fossil record of tetraonid grouse dates back to the middle Miocene, 9–6 MYA. Ancestral species evolved in temperate forests of the west Nearctic (Short, 1967), and should have embodied the ancestral form. After ancestral ruffed grouse evolved, a part of the American grouse population emigrated to Eurasia, its founding form represented by ancestral hazel grouse, "*prae-bonasia*". This species must have conserved relatively primitive characters for millions of years. Repeated invasions of American grouse to Asia across the Bering bridge gave rise to the *Falcipennnis*, *Tetrao* and *Lagopus* complexes, while the group of prairie-dwelling grouse evolved in the Nearctic.

The oldest fossil evidence for primeval hazel grouse in Europe dates back to 600 000–500 000 years ago, but distributional range changed continuously with the expansion and retreat of the ice cover during glacial-interglacial cycles. We conclude that, during a phase of extreme retreat to far east Eurasia, an isolate of these populations was trapped in woodlands close to the east rim of the Tibetan plateau. The Chinese grouse arose from this event.

If these assessments of phenotypic characters (Short, 1967; Potapov, 1985), behavior and vocalization (Scherzinger in Bergmann et al., 1996), and mtDNA sequences hold, the Chinese grouse should not only be closest to the ancestral form of its genus, but for all tetraonid grouse as well. This species, thus, is not only a faunistic treasure of remote mountain woodlands in inner Asia but also a key reference point in grouse phylogeny.

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References

Baba Y, Fujimaki Y, Klaus S, Butorina O, Drovetskii S, Koike H, 2002. Molecular population phylogeny of the hazel grouse *Bonasa bonasia* in East Asia inferred from mitochondrial control-region sequences. Wildlife Biol. 8: 251–259.

Bergmann H-H, Klaus S, Müller F, Scherzinger W, Swenson JE, Wiesner J, 1996. Die Haselhühner *Bonasa bonasia* und *B. sewerzowi*. Magdeburg: Neue Brehm-Bücherei n. 77.

Bump G, Darrow R, Edminster F, Crissey W, 1947. Ruffed Grouse. Albany: New York State Cons. Dept.

Gullion G, Martinson T, 1984. Grouse of the North Shore. Wisconsin, USA: Willow Creek Press.

Hjorth I, 1970. Reproductive behavior in Tetraonidae, with special reference to males. Viltrevy 7: 181–596.

Klaus S, Scherzinger W, Sun YH, 1996. Ökologie und Verhalten des Chinahaselhuhns *Bonasa sewerzowi*. Ornithol. Beob. 93: 343–365.

Lucchini V, Höglund J, Klaus S, Swenson J, Randi E, 2001. Historical biogeography and a mitochondrial DNA phylogeny of grouse and ptarmigan. Mol. Phyl. Evol. 20: 149–162.

Potapov R, 1985. Fauna USSR, ptitsy, otryad kyroobraznye (Galliformes), semeistvo teterevinye (Tetraonidae) 3. Leningrad: Akademia Nauka.

Short L, 1967. A review of the genera of grouse (Aves, Tetraoninae). Amer. Mus. Novit. 2289: 1–39.

Sun YH, Swenson JE, Fang Y, Klaus S, Scherzinger W, 2003. Population ecology of the Chinese grouse, *Bonasa sewerzowi*, in a fragmented landscape. Biol. Conserv. 110: 177–184.