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Why do eared-pheasants of the eastern Qinghai-Tibet plateau show so much morphological variation?

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Summary

It is known that White Eared-pheasants *Crossoptilon crossoptilon drouyni* interbreed widely with Tibetan Eared-pheasants *C. harmani* at the boundary of their ranges. A new hybrid zone has been found recently in eastern Tibet, far away from the boundary of the parental species' ranges. Based on ecological observations of eared-pheasants and the geographical history and pattern of modern glaciers, we have attributed the complex morphological variation of eared-pheasants and the high biodiversity of the eastern Qinghai-Tibet plateau to its varied geography.

Introduction

The eared-pheasant genus *Crossoptilon* is endemic to China and includes four species. The Brown Eared-pheasant *C. mantchuricum* is found in northern China and the Blue Eared-pheasant *C. auritum* occurs on the plateau of northern Qinghai-Tibet. These species show no morphological variation and have no described subspecies. The White Eared-pheasant *C. crossoptilon* shows greater variations in plumage colour and four subspecies have been recognised: *crossoptilon* in western Sichuan and south-eastern Tibet, *lichiangense* in north-western Yunnan, *drouyni* in the area between the Nujiang River and the Jinsha River, and *dolani* in Yushu of southern Qinghai. The Tibetan Eared-pheasant *C. harmani* is restricted to Tibet, north of the main axis of the Himalayas (Ludlow and Kinnear 1944). It was formerly treated as a subspecies of the White Eared-pheasant (Delacour 1977, Cheng *et al*. 1978), but more recently has been considered a full species (Sibley and Monroe 1990, Cheng 1994), mainly because of its dark blue-grey plumage, which is distinct from the predominately white plumage of the other subspecies.

The populations of the Tibetan Eared-pheasant are very uniform in plumage colour through most of the range. However, in the north-eastern boundary of their range, the birds interbreed with *drouyni* and some hybrids have been recorded (Delacour 1945, Cheng *et al*. 1978). More puzzling variations in the plumage of eared-pheasants have been found in other areas of the eastern Qinghai-Tibet plateau. Within the range of *drouyni*, individuals have been found with white spots on the black top of the head, while birds with partly, or entirely, white tail feathers have been recorded (Cheng *et al*. 1983). There are even more complicated plumage patterns in north-eastern Tibet and southern Qinghai,

where the ranges of *crossoptilon*, *drouyni* and *dolani* meet (Pack-Blumenau and Lu 1999, X. Lu pers. obs.).

This variation in eared-pheasants has also been recorded for other birds in the region, and has been attributed to the geographical complexity of the vast eastern plateau (Tang *et al*. 1996, Lu *et al*. 1998). Understanding these patterns of variation is important not only for evolutionary and systematic studies but also for conservation (Pojas 1992). However, there has been no detailed account of how the geographical conditions that are responsible for restricting gene flows among populations has led to the higher species diversity in the eastern plateau.

Observations

In May 1995, we discovered a group of hybrids between *C. c. drouyni* and *C. harmani* in a locality named Sawang in eastern Tibet (93°39′E, 32°24′N), not previously visited by biologists. The following characteristics of these hybrids are based upon field observations and two adult specimens, plus a number of moulted feathers (including 91 tail, 41 wing and 488 other feathers). The birds showed a white–blue plumage, a combination between pure white typical of *drouyni* and dark blue typical of *harmani*. Many of their primary feathers were dark, deriving from *harmani*, with a few feathers completely white or with white spots, like *drouyni*. In *drouyni*, most of the tail is white, shading into dark greenish-blue towards the tip; in *harmani*, it is greyish near the tail base, the rest being metallic blue-black. But the bases of the tail feathers of the hybrids were often spotted with white. One juvenile (about three months old) weighed 1.18 kg and showed a similar plumage pattern to the adult hybrid.

The hybrid eggs differed from those of the parents in colour and size. The mean length and breadth of nine hybrid eggs were 55.1 mm (S.D. ± 1.73) and 41.2 mm (± 1.02) respectively, significantly smaller than six eggs from *drouyni* (length 59.1 mm ± 1.46, $t = 4.56$, $P < 0.001$; breadth 43.5 mm ± 1.43, $t = 3.39$, $P < 0.005$); but more similar to 40 *harmani* eggs (length 57.3 mm ± 3.38, $t = 1.72$, $P = 0.09$, breadth 41.7 mm ± 1.01, $t = 1.29$, $P = 0.20$). Newly born hybrid chicks were similar in plumage patterns to the parents.

Topographically, Sawang comprises high mountains and deep valleys, with vertically stratified natural vegetation. Two types of forest on the south-facing slopes are the preferred habitats of the hybrids with hollyleaf-like oak *Quercus aquifolioides* at lower elevations (3,700–4,300 m) and Tibetan juniper *Sabina tibetica* higher up (4,200–4,700 m elevation) (Lu 1997).

On 3 August 1995, we left Sawang and explored the valley of the Niwuzangbu River, frequently encountering hybrids. Next day, we climbed up through the Aigagong glacier at 5,400 m and entered the next valley. Descending into the Tibetan juniper forest, we were surprised to find that the eared-pheasants had blue-grey plumage and were pure *harmani*. Eared-pheasants on opposite sides of the mountain ridge could not meet, because our observations on habitat use by the hybrids confirmed that they never strayed more than 100 m above the tree line (4,800 m elevation).

How, then, are these hybrids produced in our study area? In other words, how do the parental species, *C. c. drouyni* and *C. harmani*, interbreed? If we examine the topography and glacial structure over a more extensive range (Figure 1), it

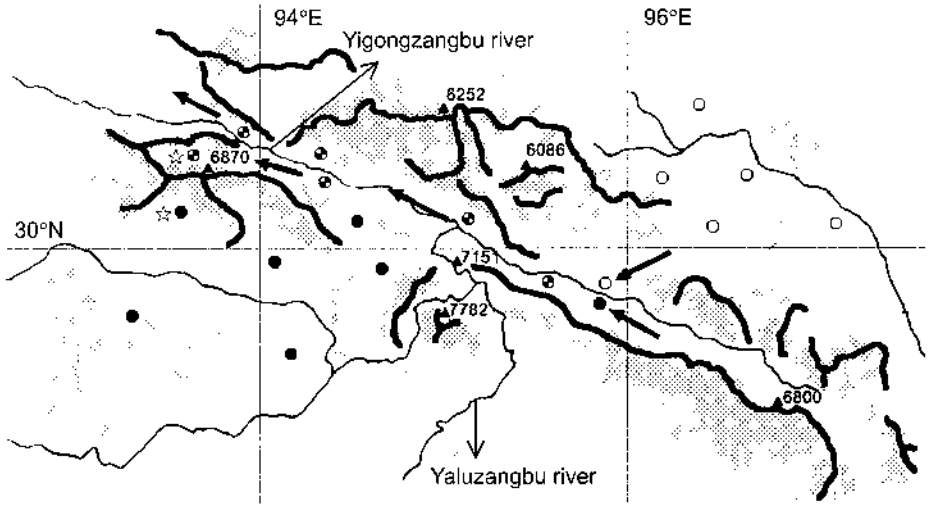

Figure 1. An inferred pattern of hybridization between two species of eared-pheasants in the eastern Tibet. Stippled areas, glaciers; thick black lines, mountain chains; triangles, mountain peak with altitude (m); filled circles, *C. crossoptilon drouyni*; open circles, *C. harmani*; quartered circles, hybrid; stars, the two sites where the hybrid and pure *harmani* were found respectively in this survey. Notice that they are separated by a mountain chain.

can be seen that the Yigongzangbu River (into which the Niwuzangbu river flows) passes through high mountains to enter the valley of the Yaluzangbu River. Here, warm humid air from the Indian Ocean collects, and maritime glaciers develop in the mid-Nianqingtanghgula mountains. The Yigongzangbu valley opens toward a bend of the Yaluzangbu River and thus forms a unique channel through which warm humid air comes into northern Tibet (Yang *et al*. 1983). To judge from earlier collections (e.g. Delacour 1945, Cheng *et al*. 1983) and data from this survey, *drouyni* and *harmani* occur on both sides of the mid-Yigongzangbu River and there is also a record of both species in sympatry at Pomi (Figure 1). It is likely that hybridization between these species occurred where their ranges met. Competing with their parents, the hybrids were forced to search for new territory. Being poor flyers, they could not cross the high mountains and glaciers in the surrounding area and had to disperse along the Yigongzangbu valley into the tributaries of the river, including the Niwuzangbu valley (Figure 1). Indeed we observed and were also informed (by Professor Gu of the Tibet Plateau Institute of Biology) that hybrids occur along the main Yigongzangbu valley.

Discussion

A hybrid zone is a region of steep genetic and phenotypic intergradation between genetically distinct and relatively uniform contiguous populations (Mayr 1963). Over 170 reasonably clear hybrid zones have been documented amongst plants and animals (Barton and Hewitt 1989), most of which occur where their parental

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species meet directly. The complicated dispersal of hybridization in eared-pheasants is especially interesting.

The fact that this hybrid population can successfully breed and is a predominant component of the local galliform community indicates that the hybrids are viable and may have been established in the area for a long time. Under the biological species concept (Mayr 1963), *harmani* cannot be a single species. However, based on the phylogenetic species concept (Cracraft 1983), the two parental taxa should be considered as distinct species that have retained the ability to interbreed (Zink and McKitrick 1995).

Comprehensive research on the natural history of the Qinghai-Tibet plateau reveals that the plateau has had a very short process of evolution (Li *et al*. 1986). During three million years from the late Tertiary to the late Quaternary, the mountains in the eastern plateau rose 3,000 m in elevation (from 1,000 to over 4,000 m), much of this change perhaps being only 100,000 years ago. These Pleistocene environmental changes made an important impact on avian microevolutionary genetic diversification (Avise and Walker 1998). The rapid and drastic geological changes in the eastern Tibetan plateau, along with an alternation between glacial and interglacial epochs since the Quaternary must have greatly affected speciation in the genus *Crossoptilon*, which possibly originated from the eastern Himalayas in the Tertiary (Lu *et al*. 1998). Small scale geographical changes could initiate speciation among these poor-flying and non-migratory pheasants. It is the contradictory coexistence of geographical barriers and riverine corridors that has produced the avian diversity in the area we observe today.

Thus far, the hypothesis is untested. Further investigations are planned to collect more data on the morphological and molecular variation of eared-pheasants, as well as more data on ecology and behaviour, throughout their range. This will allow us to evaluate hybridization and gene flow in these birds. Based on historical changes and present patterns of the environments on the plateau, we might be able to explain the real cause of this puzzling variation and clarify the evolution of eared-pheasants in this key area for nature conservation in Asia.

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