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Hybridization & Zoogeographic Patterns in Pheasants

Paul A. Johnsgard
University of Nebraska-Lincoln, pajohnsgard@gmail.com

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HYBRIDIZATION & ZOOGEOGRAPHIC PATTERNS IN PHEASANTS

PAUL A. JOHNSGARD

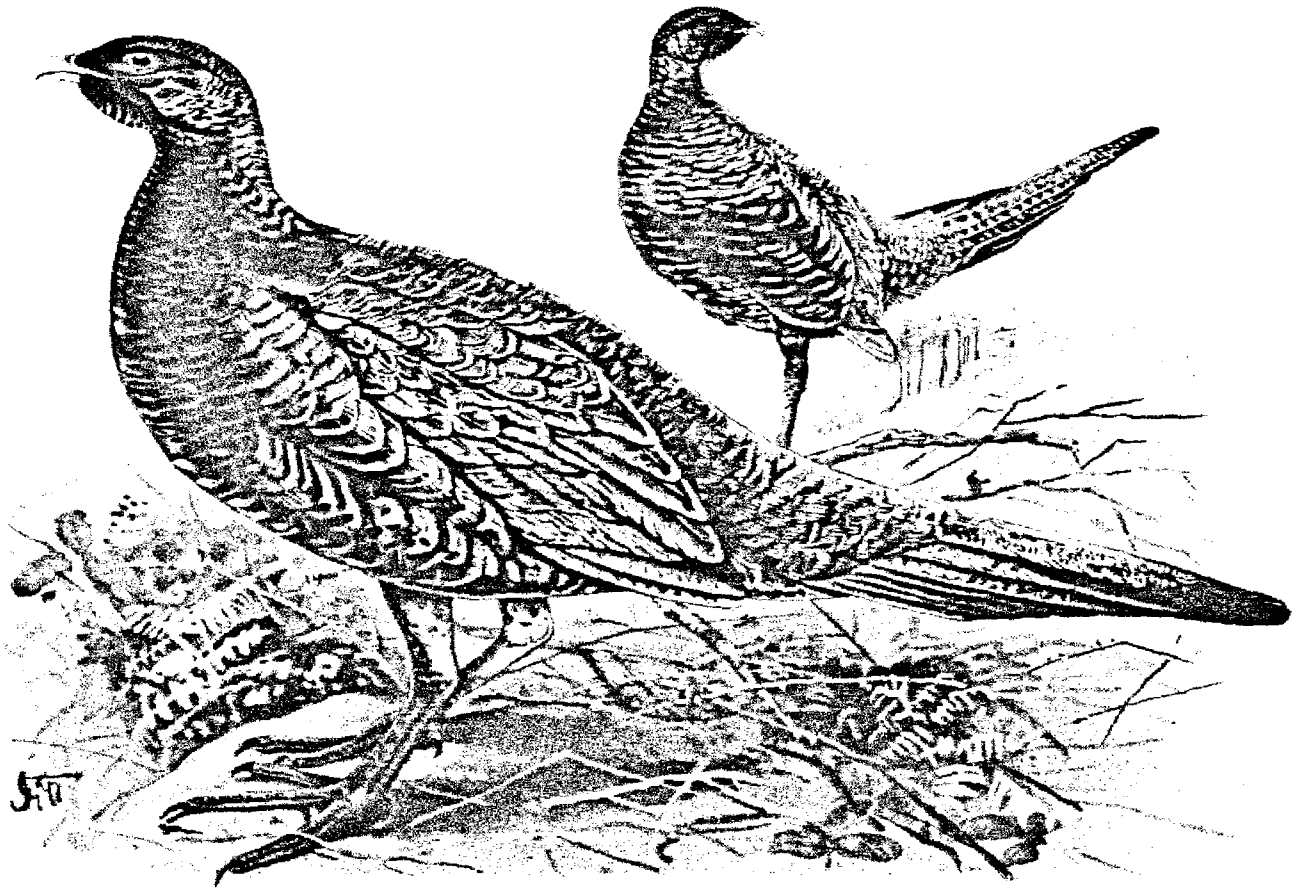
The purpose of this paper is to inform members of the W.P.A. of an unusual scientific use of the extent and significance of hybridization among pheasants (tribe Phasianini in the proposed classification of Johnsgard, 1973). This has occasionally occurred naturally, as for example between such locally sympatric species pairs as the kalij *(Lophura leucomelana)* and the silver pheasant *(L. nycthemera)*, but usually occurs "accidentally" in captive birds, especially in the absence of conspecific mates. Rarely has it been specifically planned for scientific purposes, such as for obtaining genetic, morphological, or biochemical information on hybrid haemoglobins (Brush, 1967), transferins (Crozier, 1967), or immunoelectrophoretic comparisons of blood sera (Sato, Ishi and Hiral, 1967).

The literature has been summarized by Gray (1958), Delacour (1977), and Rutgers and Norris (1970). Some of these alleged hybrids, especially those not involving other Galliformes, were inadequately documented, and in a few cases such as a supposed hybrid between domestic fowl *(Gallus gallus)* and the lyrebird *(Menura novaehollandiae)* can be discounted. My primary emphasis is on intra-tribal hybrids, together with a brief survey of reputed examples of hybridization between pheasants and species representing other tribes, subfamilies and families of the Galliformes.

Extra-tribal Hybridization —

Phasianini X Perdicini

In most classifications the pheasants and Old World partridges and their close relatives are included as members of the same subfamily (Phasianinae). Although a substantial number of hybrid records might be expected, Gray lists only three. These include crosses of *Gallus gallus (G. "domesticus"* according to Gray) with *Alectorism graeca* and *Perdix perdix*, and one between *Phasianus colchicus* and *Perdix perdix*. These were all presumed hybrids; none was produced under controlled conditions. Likewise, none was proven to be fertile, although one of the presumed *Gallus* x *Perdix* hybrid males exhibited the sexual behaviour of a "normal" domestic fowl.



'Hybrid Capercaillie and Pheasant' shot at Loch Lomond, Scotland, Dec. 1890 – from J.G. Millais, *Game Birds and Shooting Sketches,* London 1892.

Phasianini X Tetraoninae

Most extra-tribal hybrid records involving pheasants have implicated various species of grouse. Except for an unlikely hybrid reported between a black grouse *(Tetrao tetrix)* and a silver pheasant, all involved the domestic fowl or the common pheasant *(Phasianus colchicus)*.Domestic fowl have reportedly been hybridized with the ruffed grouse *(Bonasa umbellus)*, hazel grouse *(Bonasa bonasia)* and willow ptarmigan *(Lagopus lagopus*, including *L.l. scoticus)*, while pheasants have allegedly hybridized with ruffed grouse, pinnated grouse *(Tympanuchus cupido)* capercaillie *(Tetrao urogallus)*, black grouse, rock ptarmigan *(Lagopus mutus)*, red grouse *(lagopus l. scoticus)*, and blue grouse *(Dendragapus obscurus)*. Unlikely as some of these combinations might seem, at least some of them have occurred repeatedly. For example, Boback and Müller-Schwarze (1968) provided a photograph of a hybrid pheasant x black grouse, and stated that at least 15 such specimens were reported between 1833 and 1854. Likewise, Jewett (1932) and Hudson (1955) described five apparently natural hybrids between pheasants and blue grouse, dating from late in the 19th century (Anthony, 1899). Apparently no grouse x pheasant hybrid was fertile, nor showed signs

of sexual activity. Probably the relatively promiscuous mating systems of most grouse as well as of pheasants and domestic fowl have facilitated this high incidence of inter-tribal hybridization.

Phasianini X Numidinae

Crosses between pheasants and guineafowl, although unlikely, have been unquestionably obtained. Domestic fowl have reputedly been hybridized with both the vulturine guineafowl *(Acryllium vulturinum)* and the domestic guineafowl *(Numida meleagris)*, according to Gray (1958). The latter cross has also been studied biochemically by Crozier (1967), as well as by Sato, Ishii and Hiral (1967). Presumed hybrids between common pheasants and domestic guineafowl, and between the Indian peafowl *(Pavo cristatus)* and domestic guineafowl, have also been reported. Hanebrink (1973) recently described the morphology and behaviour of this combination. A fifth hybrid combination between pheasants and guineafowl was a reported cross between the Cabot's tragopan *(Tragopan caboti)* and the mitred guineafowl *(Numida mitrata)* which, like the other pheasant x guineafowl hybrids, appears to have been completely sterile.

Phasianini X Meleagridinae

Pheasant x turkey hybrids have occurred in captivity, as have domestic fowl x domestic turkey *(Meleagris gallopavo)*. Four hybrids were reportedly reared (out of a hatch of five) involving a domestic turkey and a peahen *(Pavo cristatus)*. Crosses have also been obtained by artificial insemination between common pheasants and domestic turkeys (Asmundson and Lorenz, 1955). Birds obtained by this method were sterile. Presumed "natural" hybrids of this combination have also been reported occasionally.

Phasianini X Cracidae

Some rather dubious crosses between domestic fowl and various cracids have also been reported (Gray, 1958). There is an alleged early case of apparent hybridization between a male curassow *(Crax* sp.) and a female domestic fowl, another similar case of a male *Crax alberti* hybridizing with a female domestic fowl, and a third presumed case of hybridization between the domestic fowl and a guan *(Penelope* sp.). None of these cases can be accepted without additional documentation.

Phasianini X Megapodidae

The only case of this highly unlikely cross was reported between a male scrub turkey *(Alectura lathami)* and a domestic hen (G.A. Keartland, cited by Gray, 1958). Three "alleged" hybrids were reported, including a female that laid eggs that were "not very large".

TABLE 1

Ecological distribution of pheasants in selected areas of high species density in Asia.

	High Montane Forests	Mid-montane Forests	Lowland Forests
Central Himalayas	Blood Pheasant	Koklass	Indian Peafowl
	Impeyan	Cheer Pheasant Satyr Tragopan Kalij	Red Junglefowl
Upper Burma/ Yunnan		Kalij	Red Junglefowl
		Bar-tailed Pheasant Blyth's Tragopan	Gray Peacock Pheasant Green Peafowl
Annam (Vietnam)		Silver Pheasant	Edward's Pheasant
		Imperial Pheasant	Red Junglefowl Siamese Fireback Gray Peacock Pheasant Green Peafowl Crested Argus
Malay Peninsula		Rothchild's Peacock Pheasant	Malayan Peacock Pheasant Red Junglefowl Great Argus Crested Argus Green Peafowl Crested Fireback Crestless Fireback
Sumatra		Bronze-tailed Peacock Pheasant	Great Argus
		Salvadori's Pheasant	Crested Argus Crestless Argus Red Junglefowl Malayan Peacock Pheasant
Borneo			Great Argus Crested Fireback Crestless Fireback Bornéan Peacock Pheasant Wattled Pheasant

Summary of extra-tribal Hybridization

All of the inter-familial combinations are vague and unsupported and should probably be discounted. What is surprising is the absence of any reported hybrids between the pheasants and the New World quails *(Odontophorinae)*. Even more surprisingly, there are also no reported crosses between the New World quails and the Old World partridges *(Perdicini)* although many species of both groups have bred regularly in captivity.

Intra-tribal Hybridization

Hybridization within the pheasant tribe Phasianini is far more frequent than is inter-tribal hybridization, and offers a much greater amount of information of significance from a taxonomic and ecological perspective. The summary provided here (Table 1) lists all pheasant species implicated in interspecific hybridization in the summaries of Gray (1958), Rutgers and Norris (1970), and Delacour (1977). The vernacular names and sequence of species, as well as the species limits, are those employed by Delacour. The domestic fowl *(Gallus "domesticus")* is considered conspecific with the red junglefowl *(G. gallus)*.

Several interesting conclusions can be drawn from a study of these accounts. The first is that fertility among intergeneric hybrids is relatively low, and limited to males. Male fertility has been reported for intergeneric hybrids between *Lophura* and *Crossoptilon, Lophura* and *Syrmaticus, Lophura* and *Chrysolophus, Catreus* and *Syrmaticus, Syrmaticus* and *Phasianus,* and *Phasianus* and *Chrysolophus.*

Fertility involving both sexes is apparently limited to intra-generic hybrids, such as those between species of *Tragopan, Gallus, Lophura, Crossoptilon, Syrmaticus, Phasianus, Chrysolophus,* and *Pavo*. Only three definite cases of extensive natural hybridization under wild conditions are so far known among pheasants. These involve the red and Sonnerat's *(Gallus sonnerati)* junglefowls, the kalij and silver pheasants, and the white *(Crossoptilon crossoptilon)* and blue *(C. auritus)* eared pheasants. The golden *(Chrysolophus pictus)* and Lady Amherst's *(C. amherstiae)* pheasants are not yet known to come into contact in the wild, but hybridize readily in captivity producing fertile hybrids of both sexes (Phillips, 1921; Danforth and Sandness, 1939; Danforth, 1950).

Table 1 also suggests that *Gallus* exhibits no intergeneric hybrid fertility. *Gallus* occupies a somewhat isolated position in the pheasant tribe; additionally the authenticity of the fertile hybrid between a domestic fowl and a scrub turkey is highly questionable in the basis of its lack of intratribal hybrid fertility.

On the other hand, the genus *Lophura* seems to occupy a relatively central position in the pheasant assemblage, with hybrid combinations extending on the one extreme to the genus *Tragopan*, and on the other to *Chrysolophus* and the other "long-tailed" pheasant genera. The peafowl and peacock pheasants seem to be relatively isolated, however, with sterile hybrids reported between *Pavo* and the genera *Gallus* and *Phasianus* (Gray, 1958) as well as with *Lophophorus* (Delacour, 1977). So far, hybridization involving the genus *Polyplectron* seems to be limited to crosses between the obviously very closely related gray *(P. bicalcaratum)* and Germain's *(P. germaini)* peacock phea-

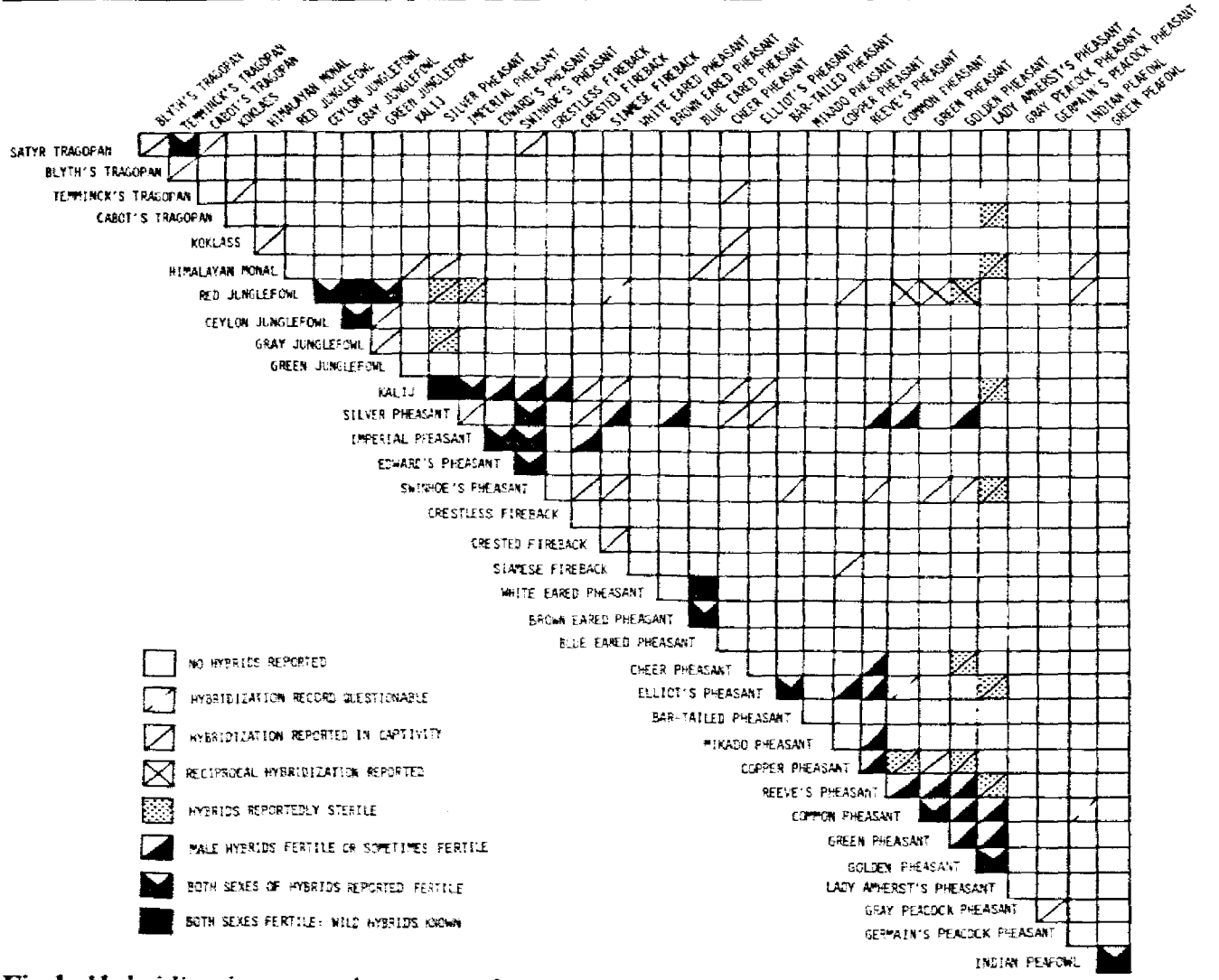


Fig 1. Hybridization records among pheasants. Records for the domestic fowl are included under red jungle fowl.

sants (Delacour, 1977). Genera that so far have not been reported to be involved in hybridization include *Ithaginis, Pucrasia, Rheinartia, Argusianus,* and *Afropavo*. Of these, all but *Pucrasia* are only rarely kept and bred under captive conditions.

Summary of Intra-tribal Hybridization

Of the calculated 1128 mathematically possible interspecific crosses that are possible within the 48 species of Phasianini, a total of 91 have actually been reported to have occurred, or 8.1 percent of the possible total. This compares with 15 of 120 total possible combinations (12.5 percent) among the 16 species of grouse (Tetraoninae) as reported by Johnsgard (1982). Further, a total of 35 of the 48 pheasant species have been implicated in hybridization, or 73 percent of the total tribe, while in the grouse subfamily 12 of 16 species, or 75 percent, have been so implicated. Of the pheasant hybrids, 46.2 percent

have been intrageneric on the basis of current taxonomy and 53.8 percent intergeneric, while 42 percent (38 of 91) have been reported as being at least occasionally fertile. By comparison, 10 of the 15 known grouse combinations, or 67 percent, are intergeneric by current taxonomic standards, and only 33 percent intrageneric. Most of these latter hybrids were of wild birds, and thus their fertility is not generally known.

Distributional Patterns

The entire subfamily Phasianinae (Perdicini and Phasianini as recognized here) is centered in the Oriental zoogeographic region. Except for the single anomalous case of *Afropavo* in Africa, all the pheasants are limited to southeastern Asia, roughly between the Black Sea on the west and Japan on the east, and extending northwards as far as Mongolia, and south to the Lesser Sundas. If the collective native ranges of all the pheasants are plotted on a map (which is made somewhat difficult because of uncertainties as to the original range limits of *Phasianus colchicus* and *Gallus gallus,* this geographic relationship becomes very clear (Figure 2). For example, some 45 species of Phasianinae (18 Phasianini and 27 Perdicini) out of an approximate world

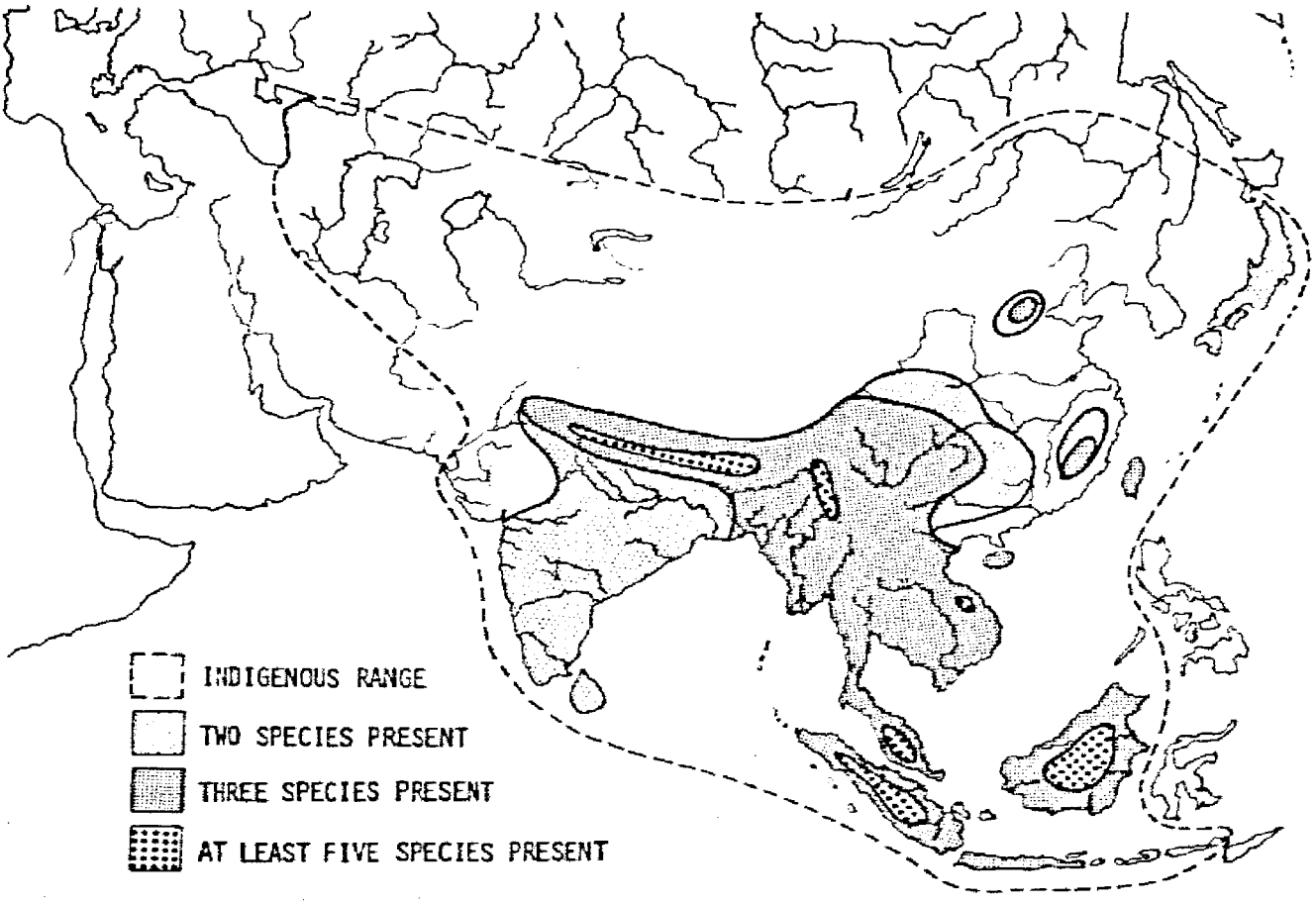


Fig 2. Species-density distribution map of the pheasants, excluding introduced ranges.

total of 174, or more than 25 percent, are native to the Indian subcontinent (Ali and Ripley, 1978). By comparison, sub-Saharan Africa has only a single species and genus of pheasant, but supports 40 additional species of Perdicini, nearly all francolins. The central Himalayas, as represented by Nepal, support 14 species of Perdicini and 8 pheasants (Fleming *et al.*, 1976). Southeastern mainland Asia (Burma to the South China Sea) supports 39 species (16 Perdicini, 23 Phasianini) (King and Dickinson, 1975).

Beyond these overall range aspects, some areas are high in species diversity of pheasants, based on available information on individual species' ranges (Figure 2). Several areas support five or more pheasant species. Eight pheasant species occur in the Himalayan mountains. These include all of the most alpine-adapted and partridge-like of the pheasants, including the genera *Ithaginis, Tragopan,* and *Pucrasia* (Table 1).

Northern Burma and adjacent Yunnan, in the upper reaches of the Yangtze, Mekong, Salween, and Irrawaddi rivers support six pheasant species. In these temperate-zone mountain valleys such essentially tropic-adapted genera as *Polyplectron* and *Pavo* exist in fairly close proximity to more montane-adapted types such as *Tragopan*. Annam (now central Vietnam) supports eight pheasant species, including two *(Lophura imperialis* and *L. edwardsi)* whose ranges apparently are the most limited of any mainland pheasant species. Delacour (1977) considered their closest living relative to be the Swinhoe's pheasant *(L. swinhoei)*, but zoogeographically it is more probable that they are offshoots of a generalized mainland kalij-like ancestor.

The Malay Peninsula, from southern Burma (Tenasserim) southward, supports eight native pheasant species, including one endemic *(Polyplectron inopinatum)* and one species shared only with Sumatra *(Polyplectron malaccensis)*. This area would seem to be the center of evolutionary diversity of the highly specialised peacock-like pheasants *(Pavo, Argusianus, Rheinartia* and *Polyplectron),* in the same way that the Himalayas obviously have served as the ancestral home of the more partridge-like genera. The presence of an archipelago situation (Greater and Lesser Sundas plus Borneo) has probably facilitated speciation in this area. Both Borneo and Sumatra thus qualify as major centers of species diversity in pheasants, supporting seven and five species respectively. Sumatra's pheasant fauna includes two endemics *(Polyplectron chalcurum* and *Lophura salvadori),* while Borneo likewise supports two endemics *(Lophura bulweri* and *Polyplectron schleiermacheri,* the latter considered by Delacour as only subspecifically differentiated). This general region from Malaya to Borneo also supports several endemic and distinctive genera of Perdicini *(Haematortyx, Caloperdix, Rhizothera, Melanoperdix),* further attesting to its importance as a center of phasianine evolutionary diversity.

Summary

A review of interspecific pheasant hybrids as reported in the literature reveals a relatively high rate of hybridization in captivity but a low rate of hybridization in the wild. All of the 91 known hybrid combinations have been reported from captivity, and three of these combinations have also been reported from the wild. All of the latter involve species pairs of known close relationships (red and gray junglefowl, kalij and silver pheasant, and white and blue eared pheasant), suggesting that reproductive isolating mechanisms in the pheasants are much more effective under natural conditions than are those of grouse, a group in which hybridization under natural conditions is relatively frequent. An analysis of pheasant distribution patterns indicates that the highest levels of natural species diversity occur in the central Himalayas, in the Upper Burma and Yunnan area, in central Vietnam, on the Malay Peninsula, and in Sumatra and Borneo. No single area of evolutionary origin of the pheasants is apparent from this analysis.

ZUSAMMENFASSUNG/RÉSUMÉ/SAMENVATTING

Ein Überblick über die in der Literatur berichteten zwischenartlichen Bastardierungen bei Fasanen zeigt, daß Gefangenschaftszuchten sehr häufig Bastardierungen aufweisen, während das in der freien Wildbahn viel seltener der Fall ist. Alle 91 bekannten Bastardierungen kommen in Gefangenschaftszuchten vor, aber nur 3 sind in der Wildbahn anzutreffen Isolationsmechanismen sind unter natürlichen Bedingungen sehr viel wirksamer, dennoch kommt es bei den Schneehühnern (grouse) relativ häufig zu Bastardierungen. Eine Untersuchung von Verteilungsmustern bei Fasanen zeigt, daß die größte Verschiedenheit bei den Fasanenarten im Himalajagebiet vorkommt.

Un aperçu des croisements entre diverses espèces de faisans décrits dans la littérature révèle un nombre relativement important de cas d'hybridation en captivité mais par contre un nombre restreint en liberté. Les 91 cas de combinaisons seulement ont été également notées en liberté. Ces derniers cas se rapportent tous à des couples d'espèces très proches (coq Bankiva et coq Sonnerat, faisan leucomèle et faisan argenté, hoki blanc et hoki bleu) ce qui fait supposer que les mécanismes isolants de reproduction chez les faisans sont plus efficaces dans des conditions naturelles que chez les tétraonidés, groupe dans lequel l'hybridation dans des conditions naturelles est relativement fréquente. Une analyse de la distribution des dessins et formes indique que les plus hauts niveaux de diversité chez les espèces naturelles ont lieu dans l'Himalaya central.

Een overzicht van interspecifieke fazanten die tot hybridisatie kunnen overgaan, zoals gerepporteerd in de literatuur, laat zien dat dit in gevangenschap veel is gebeurd en maar in een enkel geval in de vrije natuur. Elke van de 91 bekende hybride combinaties zijn gerapporteerd uit de gevangenschap en maar drie van deze combinaties zijn ook in het wild aangetroffen. En deze laatste zijn nauw verwant (Rood Boshoen en Sonnerathoen, de groep van de Kalij fazanten en de Zilverfazanten en de Witte en de Blauwe Oorfazant), zodat veronderstelt kan worden dat het reproductieve isolatiemechanisme bij fazanten veel sterker is onder natuurlijke omstandigheden dan bij ruigpoothoenders, een groep waarbij hybridisatie tamelijk vaak voorkomt. Een analyse van de verspreidingspatronen van fazanten toont aan dat de hoogste graad van naturlijke soortverscheidenheid voorkomt in het centrale Himalayagebergte.

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PROFESSOR PAUL A. JOHNSGARD, THE UNIVERSITY OF NEBRASKA-LINCOLN, LINCOLN, NEBRASKA 68588, U.S.A.