Biological Journal of the Linnean Society, 2003, **80**, 573–600. With 3 figures

Hybrid origin of the imperial pheasant *Lophura imperialis* (Delacour and Jabouille, 1924) demonstrated by morphology, hybrid experiments, and DNA analyses

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Received 20 September 2002; accepted for publication 22 May 2003

The imperial pheasant *Lophura imperialis* was described in 1924 from a captive pair that was obtained in Vietnam, and that became the sole founders of a captive line in France. Always considered a highly endangered and mysterious species, and despite concerted searches, *L. imperialis* was not found again in the wild until one was trapped in 1990, and the captive population gradually died out. Its status as a distinct species was unquestioned until the late 1990s when the possibility of a hybrid origin was raised. To elucidate the taxonomic status of *L. imperialis*, we studied all the existing museum specimens, carried out captive hybridization experiments, and analysed mitochondrial DNA and microsatellites. All these lines of evidence demonstrate congruently and conclusively that *L. imperialis* is an occasional hybrid between silver pheasant *L. nycthemera* and Edwards's pheasant *L. edwardsi,* with the 1990 bird probably being a hybrid between *L. nycthemera* and Vietnamese pheasant *L. hatinhensis*. Thus *L. imperialis* has no taxonomic standing and should be removed from lists of species of conservation concern. However, hybridization with *L. nycthemera* may pose a further threat to the survival in the wild of the endangered *L. edwardsi* and *L. hatinhensis*. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, **80**, 573–600.

ADDITIONAL KEYWORDS: conservation – Edwards's pheasant – fragmented habitat – hybridization – microsatellites – morphological analyses – mtDNA sequencing – silver pheasant.

INTRODUCTION

The discovery of the imperial pheasant *Lophura imperialis* was perhaps the high point of J. Delacour's expeditions to central Annam (Delacour & Jabouille, 1925). In 1923, he had obtained a single live pair of a heretofore unknown captive pheasant from missionaries, who said the birds had been obtained on the southern boundary of the Quang Binh province, northern Quang Tri, Vietnam (Delacour & Jabouille, 1925). The species was named in honour of Khaï Dinh, Emperor of Annam (Delacour & Jabouille, 1924). The pair was sent to Delacour's estate in France in 1924 and the following year began producing young (Delacour, 1925). However, further attempts to locate *L. imperialis* in the wild were unproductive. Father Meaunier, a French missionary, was said to have obtained a few more individuals (Delacour, 1977), but these died en route to France and their identity was never verified. In 1938, C. Cordier, a famous collector of live birds, attempted and failed to procure *L. imperialis* (Delacour, 1977). In the late 1930s B. Björkegren spent two weeks searching for it without result (Eames & Ericson, 1996). For many years after that time, until recently, much of Vietnam was inaccessible to ornithologists, and the lack of further reports of *L. imperialis* did not seem a cause for great concern.

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Although *L. imperialis* has been repeatedly said to occur in central Laos (Delacour & Jabouille, 1931; David-Beaulieu, 1949; King, Dickinson & Woodcock, 1975), no specimens exist from that country, and its putative occurrence was based only on vague descriptions by local hunters. Recent field surveys in Laos have resulted in no further records (McGowan & Garson, 1995), and the past or current occurrence of *L. imperialis* in Laos is highly doubtful. *Lophura imperialis* has also been included on the Chinese list (Xu *et al.*, 1996), presumably in error. The species is therefore definitely known only from Vietnam, where it must be an extremely rare endemic, and as such has been the subject of great conservation concern (Collar, Crosby & Stattersfield, 1994; McGowan & Garson, 1995; Fuller & Garson, 2000). Despite the recent conservation concern and field efforts to find a wild population, the only other records are of two live immature males, one in 1990 (Robson *et al.*, 1993; Eames, Lambert & Nguyen, 1994) and the second in 2000 (BirdLife International, 2000). However, both of these recently trapped individuals differ distinctly from other specimens in some features (Appendix; Vo Quy, unpubl. data), and no populations have been located in the areas where these individuals were found.

Despite the fact that Delacour's original pair had founded a captive population of *L. imperialis*, and although some of their progeny had been distributed to other aviaries, they failed to thrive and nearly died out. By 1959 the only known birds remained in Antwerp Zoo, where these few were hybridized with the silver pheasant *L. nycthemera* and with Edwards's pheasant *L. edwardsi* in an attempt to recreate new stock (Carpentier *et al.*, 1975). Although some resultant hybrid individuals closely resembled the description of the original pair, others looked more like the parental species, and the stock was highly variable. The population's genetic purity had obviously been seriously compromised, and attempts to sustain the 'species' in captivity failed, later pairings resulting only in male progeny (Carpentier *et al.*, 1975), a seeming catastrophe for the survival of the species.

Delacour wrote that *L. imperialis* occurs only in the dense forests of the mountains of the interior of the Province of Dong Hoi, Vietnam (Delacour & Jabouille, 1931), but the source of his information is uncertain. In fact, this conflicts with both recent records, which were located in lowland secondary forest. On 28 February 1990, a wild-trapped bird was obtained in lowland forest 12 km west of Cat Bin, approximately 200 km north of Dong Hoi in the same snare line as two adult male Vietnamese pheasants *L. hatinhensis* (Robson *et al.*, 1993), an endemic species closely related to *L. imperialis*. On 27 February 2000, another individual considered to be *L. imperialis* was obtained in Da Krong district, Quang Tri province, within the historical range of *L. edwardsi*, yet another endemic and closely related species of secondary lowland forest (Truong Van La, pers. comm.; Dang Gia Tung, pers. comm.; Huynh Van Keo, 1999). Thus, *L. imperialis* is evidently sympatric with two other congeneric pheasant species, all endemic to a small area in Annam and sharing the same habitat, a remarkable situation, especially among large-bodied birds. Although wild populations are known for both *L. hatinhensis* and *L. edwardsi*, all attempts to find more *L. imperialis* other than those detailed above have failed. Thus, *L. imperialis* was considered a critically endangered Vietnamese endemic species with no known wild population and none in captivity (McGowan & Garson, 1995; Garson, 1998; BirdLife International, 2000; Fuller & Garson, 2000). More recently it was treated as 'data deficient' (BirdLife, 2001) on the basis of evidence presented herein.

In 1997, K. Wood (pers. comm.) suggested that, rather than being an individual species, *L. imperialis* might actually be a hybrid between *L. edwardsi* and *L. diardi*, an idea that would explain its extreme rarity and the inability of field workers to locate a wild population. This led one of the authors (P.R.) to examine the possibility of a hybrid origin of *L. imperialis*. She found that female *L. imperialis* are intermediate between female *L. edwardsi* and *L. nycthemera* of Vietnamese races, and lack characters indicative of *L. diardi*, while the male *L. imperialis* phenotype is typical of hybrids between a glossy black and a more elaborately plumaged species of *Lophura* (Rasmussen, 1998, 1999). She also found that plumage features and anomalies of *L. imperialis* specimens are all present in the hybridized Antwerp Zoo birds, and that the *L. imperialis* phenotype shows no novel features or characters not expected from a cross between *L. edwardsi* and *L. nycthemera* (Rasmussen, 1998, 1999). After these museum studies indicated the strong likelihood that *L. imperialis* was a hybrid between *L. nycthemera* and *L. edwardsi*, another of the authors (A.H.) carried out controlled hybridization experiments in captivity for the purposes of confirmation. Simultaneously, a third author of this study (E.R.) and colleagues were exploring the molecular phylogenetics of the three endemic Vietnamese lowland *Lophura* species with the objective of contributing information vital to the process of defining a programme for their global conservation (Hennache, Randi & Lucchini, 1999). The purpose of this paper is to present the results of three different lines of inquiry into the origins and status of *L. imperialis*: morphological studies, hybridization experiments, and genetic analyses.

MATERIAL AND METHODS

The original description of *L. imperialis* was based solely on the living captive pair that Delacour brought to France from Vietnam (Delacour & Jabouille, 1924). The female holotype died in September 1927 and was preserved as Museum National d'Histoire Naturelle (MNHN) no. 1928–1117. The male holotype, which was still living at Clères in 1939, was lost along with its progeny during World War II and thus no male holotype specimen exists, nor do there appear to be any photographs of this individual. Thus we were able to make direct comparisons with the female holotype, but for males we were limited to comparisons with the rather vague type description and the first-generation male progeny.

Several of the progeny of the original pair have been preserved at the MNHN and at the Natural History Museum (BMNH), Tring, UK (see Appendix for a complete listing). Delacour also sent live descendants to American breeders, and some of these skins are preserved in US museums; however, as the lineage of most of these is unclear and interspecific hybridization was taking place from early on, these have been used advisedly. Only those progeny that are labelled as definitely resulting from the original pairing have been considered true *L. imperialis*.

Photographs of the 1990 wild-trapped immature male, both before and after its death, were sent by J. Eames, and the specimen was examined by A.H. in 1997 and 1999. A description and photographs of the living immature male wild-trapped in 2000 were sent to us by Prof. Vo Quy.

Morphological analyses

For all known museum specimens of *L. imperialis* (see Appendix), numerous close-up photographs were taken by P.R. to document external morphology. Measurements (to the nearest mm) were taken by P.R. when possible for each fully grown specimen of many characters, of which the following were measurable on most specimens and so were used for this study: bill length from nares; bill height from nares; upper mandible width from nares; central length of lower mandible; proximal width of lower mandible from feathers; crest length; flattened wing length; outer primary length; outer primary width; tarsus length; tarsus proximal depth; tarsus proximal width; tarsus minimum width; tarsus minimum depth; tarsus distal width; tail length; outer rectrix width; inner rectrix width; tail graduation (distance between tip of inner rectrix and tip of outer rectrix); greatest width of longest uppertail coverts. Many of the *L. imperialis* specimens were damaged in some way related to their captivity, often with overgrown bills, very worn or otherwise abnormal claws, and broken tails and wingtips, making it impossible to measure these characters. Photographs and measurements were also taken of several frozen and one mounted specimen(s) of the hybrids produced at the Antwerp Zoo. For comparison, photographs and the same measurements were taken of a series of Vietnamese races of *L. nycthemera* and of *L. edwardsi*. In addition, photographs were taken of a series of well-documented hybrid *Lophura* specimens in the BMNH. No specimens of *L. hatinhensis* were available for measurement, but many photographs were taken of a captive pair in the Antwerp Zoo, and of their immature offspring. Photographs and measurements of the captive hybrids at Clères (see below) were taken by P.R. when the birds were *c.* 1 year old (full-sized). Measurements taken by J. Eames of the 1990 specimen and considered to be comparable with those taken by P.R. were included. Univariate statistics and principal components analyses (PCA) were done using Systat 5.0. Characters used in PCA were: culmen length, crest length, wing length, tarsus length, and tail length. These characters were chosen to allow the inclusion of the maximum number of specimens in the analysis. Because specimens at different museums could not readily be directly compared with one another, P.R. used her photographs of each individual to construct the Appendix. In several cases, some individual characters were not visible or discernible in the photographs, so these cells were labelled 'not recorded' in the Appendix.

Captive-breeding experiments

In 1998, A.H. set up a hybridization experiment at the Zoological Park of Clères, France (Delacour's former estate) with the aim of assessing the initial results from museum studies (summarized in Rasmussen, 1998). A captive-reared male *L. nycthemera berliozi* was mated using artificial insemination with a captive-reared female *L. edwardsi*, and five chicks were produced from this cross, of which four were males and one was a female. One of the males died at 1 year of age when it was killed by two of its siblings.

Each of the resultant hybrids was studied from chick stage to adulthood, and photographs were taken at different stages of growth. Their phenotypes at 2 years of age are described herein by A.H. and are compared with those of Delacour's description and with the existing specimens of *L. imperialis* from the original pair and their progeny. The hybrids' phenotypes at about 1 year of age were also described from photographs taken by P.R., and these data are included in the Appendix.

Table 1. *Lophura imperialis* sampled for the genetic analyses

Sample ID	Sample	Origin	Captive/ wild	Sex M/F	Reference	Comments
LIM8	Feather	Quang Tri Province	W	M	Sample from J. Eames	Trapped on 27 February 2000
LIM9	Feather	Quang Tri Province	W	M	Sample from Vo Quy	Trapped on 27 February 2000 (same individual as LIM8)
LIM11	Skin and toe pad fragments	MNHN	C (F1)	M	1936–1548	Died at Clères 15/04/1936
LIM12	Skin and toe pad fragments	MNHN	C (F1)	M	1931–144	Born 1930; died at Clères 15 March 1931
LIM13	Skin and toe pad fragments	MNHN	C	M	1934–1388	Died at Clères
LIM14	Skin and toe pad fragments	MNHN – Dong Hoi	W	F	Syntype 1928–1117	Died at Clères September 1927
LIM15	Skin and toe pad fragments	MNHN	C	F	1934–1389	Died at Clères
LIM16	Skin and toe pad fragments	MNHN	C	Young F	1927–2376	Donation from Delacour 19 July 1927
LIM17	Toe pad fragment	BMNH	C	M	1931.5.11.5	Died at Clères 01 May 1931
LIM18	Toe pad fragment	BMNH	C	F	1948.70.1	Died at Clères
LIM19	Toe pad fragment	BMNH	C	Juvenile	1926.9.9.3	Died at Clères 25 August 1926
LIM20	Toe pad fragment	BMNH	C	Fledgling	1930.6.12.2.	5 weeks old; died in captivity 20 June 1930

DNA ANALYSES

DNA extraction, amplification and sequencing

Total DNA was extracted from 95% ethanol-preserved tissue or feather root samples, using procedures described by Randi & Lucchini (1998). The 5′ domain of the mitochondrial DNA control region (mtDNA CR) was PCR-amplified and sequenced as previously described (Randi & Lucchini, 1998; Randi *et al*., 2001). CR sequences were obtained from the *L. imperialis* samples listed in Table 1, and from *L. edwardsi* ($N = 6$), *L. hatinhensis* ($N = 15$), and two closely related outgroups *L. nycthemera* ($N = 4$), and *L. swinhoei* (Swinhoe's pheasant, $N = 2$). The CR sequences were aligned using CLUSTAL X with the default options (Thompson *et al*., 1997). Phylogenetic analyses were performed using the software PAUP* (Swofford, 1998), by: (1) a maximum-parsimony procedure (Swofford, 1998), excluding all uninformative nucleotide positions, with unordered and equally weighted characters; (2) the neighbour-joining algorithm (Saitou & Nei, 1987), with Tamura & Nei's (1993) DNA distances (TN93). Robustness of the phylogenies was assessed by bootstrap percentages (BP; Felsenstein, 1985), with 1000 random resamplings with replacement. Details on phylogenetic analyses are given in Randi *et al.* (2001).

Microsatellite analyses

All samples were genotyped by PCR amplification of nine microsatellites that were originally isolated at Wageningen University from the chicken (*Gallus gallus*) genome. The primers used were: M1 = MCW160; M2 = MCW236; M3 = MCW292; M4 = MCW239; M5 = MCW297; M6 = MCW254; M7 = MCW152; M8 = MCW262; M9 = MCW199. Primer sequences and information on MCW markers can be retrieved at http://www.zod.wau.nl/abg/index.html. Allelic variability was determined in DNA extracted from the *L. imperialis* samples listed in Table 1, and from *L. edwardsi* ($N = 10$), *L. hatinhensis* ($N = 5$), *L. leucomelana* ($N = 2$), *L. nycthemera* ($N = 10$) and *L. swinhoei* ($N = 3$). Each PCR amplification was performed in a total volume of 9 μL using 30–50 ng DNA, in a Perkin-Elmer 9600 Gene-Amp cycler with the following cycle: 94°C × 2 min; 30 cycles at 94°C × 30 s, 45–65°C × 30 s (depending on the optimal primer annealing temperature), and 72°C × 1 min; 72°C × 10 min. Genotypes were deter-

Table 2a. Univariate statistics for all known fully grown *Lophura imperialis* male specimens and hybrids, and comparative series of *L. edwardsi* and Vietnamese races of *L. nycthemera*

	L. imperialis						
Variable	All	Original series	Antwerp hybrids	Cat Bin	Clères hybrids	*L. edwardsi*	*L. nycthemera*
Bill length	18.2 ± 1.5 (15)	17.1 ± 1.9 (4)	17.9 ± 1.2 (7)	19.0 (1)	19.5 ± 0.6 (4)	17.7 ± 1.8 (12)	20.7 ± 1.5 (14)
Bill height	11.2 ± 0.9 (13)	10.4 ± 0.5 (5)	11.7 ± 0.5 (9)	–	–	9.9 ± 1.0 (16)	12.4 ± 0.5 (11)
Upper mandible width	10.1 ± 0.9 (15)	9.9 ± 0.7 (6)	10.4 ± 0.9 (10)	–	–	9.3 ± 0.6 (24)	11.1 ± 0.6 (14)
Lower mandible central length	11.7 ± 1.3 (12)	11.4 ± 1.1 (5)	11.9 ± 1.4 (8)	–	–	11.7 ± 0.7 (24)	13.4 ± 0.5 (13)
Lower mandible proximal width	12.3 ± 0.9 (10)	12.5 ± 0.9 (5)	12.2 ± 0.8 (6)	–	–	11.8 ± 0.7 (24)	14.1 ± 0.6 (14)
Crest length	41.1 ± 12.6 (19)	39.6 ± 8.2 (6)	42.5 ± 13.0 (9)	70.0 (1)	33.5 ± 4.3 (4)	28.6 ± 2.9 (23)	63.3 ± 6.7 (14)
Wing length (flattened)	232.9 ± 12.7 (19)	232.8 ± 7.9 (5)	229.5 ± 14.5 (10)	252.0 (1)	237.7 ± 8.3 (4)	227.9 ± 8.1 (22)	251.7 ± 1.0 (15)
Outer primary length	120.1 ± 12.0 (8)	125.7 ± 4.3 (4)	114.5 ± 15.3 (4)	–	–	117.2 ± 9.1 (16)	134.3 ± 8.4 (9)
Outer primary width	20.0 ± 0.9 (4)	20.0 ± 0.9 (4)	–	–	–	17.1 ± 1.5 (12)	19.0 ± 2.5 (12)
Tarsus length	81.7 ± 17.9 (19)	81.5 ± 6.1 (6)	78.4 ± 6.6 (9)	103.0 (1)	83.2 ± 3.5 (4)	75.7 ± 4.8 (24)	87.2 ± 5.2 (14)
Tarsus proximal depth	12.6 ± 0.9 (7)	12.7 ± 1.0 (6)	12.2 (1)	–	–	11.5 ± 0.8 (24)	13.2 ± 1.2 (13)
Tarsus proximal width	13.2 ± 1.0 (10)	12.5 ± 0.8 (5)	12.5 (1)	–	14.1 ± 0.3 (4)	11.6 ± 0.7 (22)	13.7 ± 0.9 (14)
Tarsus minimum width	6.0 ± 0.3 (10)	5.8 ± 0.4 (6)	–	–	6.2 ± 0.2 (4)	5.5 ± 0.5 (24)	6.3 ± 0.5 (14)
Tarsus minimum depth	9.8 ± 0.5 (6)	9.8 ± 0.5 (5)	9.7 (1)	–	–	8.8 ± 0.6 (22)	10.0 ± 0.8 (13)
Tarsus distal width	12.8 ± 1.1 (10)	12.3 ± 1.0 (5)	13.0 (1)	–	13.5 ± 1.0 (4)	11.7 ± 0.6 (23)	13.4 ± 1.1 (13)
Tail length	258.2 ± 38.3 (14)	256.0 ± 29.5 (6)	254.3 ± 50.1 (6)	303.0 (1)	250.0 (1)	207.5 ± 17.6 (18)	305.1 ± 56.6 (14)
Outer rectrix width	28.4 ± 5.2 (14)	30.0 ± 6.5 (5)	26.7 ± 4.3 (7)	–	27.5 ± 3.5 (2)	27.2 ± 2.1 (20)	31.1 ± 3.3 (14)
Inner rectrix width	43.0 ± 5.5 (14)	46.5 ± 2.8 (5)	40.8 ± 6.6 (7)	–	42.0 ± 1.4 (2)	38.9 ± 3.8 (21)	54.0 ± 7.3 (14)
Tail graduation	143.3 ± 35.5 (11)	154.0 ± 20.5 (5)	142.6 ± 44.2 (5)	–	–	112.0 ± 11.2 (19)	206.8 ± 54.8 (14)
Uppertail coverts greatest width	40.6 ± 5.7 (10)	42.7 ± 6.0 (3)	39.2 ± 5.5 (8)	–	–	34.4 ± 3.4 (15)	44.0 ± 4.1 (9)

Table 2b. Univariate statistics for all known fully grown *Lophura imperialis* female specimens and hybrids, and comparative series of *L. edwardsi* and Vietnamese races of *L. nycthemera*

	L. imperialis					
Variable	All	Original series	Antwerp hybrids	Clères hybrids	*L. edwardsi*	*L. nycthemera*
Bill length	16.8 ± 0.9 (6)	16.9 ± 0.9 (4)	15.9 (1)	18.0 (1)	17.9 ± 1.3 (7)	19.0 ± 0.7 (10)
Bill height	9.7 ± 0.7 (6)	9.5 ± 0.5 (5)	10.8 (1)	–	9.5 ± 0.6 (4)	11.2 ± 0.6 (7)
Upper mandible width	9.3 ± 0.4 (6)	9.2 ± 0.2 (5)	10.9 (1)	–	9.1 ± 0.8 (7)	10.1 ± 0.4 (10)
Lower mandible central length	11.3 ± 0.5 (6)	11.3 ± 0.6 (5)	11.6 (1)	–	11.0 ± 0.1 (5)	12.2 ± 0.8 (9)
Lower mandible proximal width	11.2 ± 1.1 (6)	11.2 ± 1.2 (5)	11.3 (1)	–	10.7 ± 0.5 (6)	12.9 ± 1.1 (11)
Crest length	23.1 ± 4.7 (7)	21.7 ± 4.0 (5)	30.7 (1)	23.0 (1)	17.2 ± 2.9 (8)	44.6 ± 11.8 (11)
Wing length (flattened)	224 ± 8.3 (4)	229.5 ± 0.7 (2)	212.0 (1)	225.0 (1)	213.9 ± 10.7 (8)	233.1 ± 9.6 (10)
Outer primary length	121.7 ± 7.6 (3)	126.0 ± 1.4 (2)	113.0 (1)	–	105.5 ± 8.3 (4)	123.3 ± 4.8 (9)
Outer primary width	18.3 ± 0.3 (3)	18.3 ± 0.3 (3)	–	–	16.1 ± 1.5 (7)	18.9 ± 1.4 (10)
Tarsus length	72.7 ± 4.5 (6)	71.2 ± 3.3 (4)	80.3 (1)	71.0 (1)	66.2 ± 4.1 (9)	77.3 ± 3.5 (11)
Tarsus proximal depth	11.3 ± 0.4 (4)	11.3 ± 0.4 (4)	–	–	10.2 ± 0.6 (8)	11.4 ± 0.8 (10)
Tarsus proximal width	11.4 ± 0.8 (5)	11.0 ± 0.3 (4)	–	12.7 (1)	10.7 ± 0.8 (8)	12.1 ± 0.6 (11)
Tarsus minimum width	5.4 ± 0.3 (5)	5.3 ± 0.2 (4)	–	5.7 (1)	4.9 ± 0.3 (9)	5.6 ± 0.3 (11)
Tarsus minimum depth	7.9 ± 0.5 (4)	7.9 ± 0.5 (4)	–	–	7.7 ± 0.5 (7)	8.8 ± 0.6 (11)
Tarsus distal width	11.3 ± 0.5 (5)	11.1 ± 0.3 (4)	–	12.0 (1)	10.8 ± 1.0 (8)	12.3 ± 0.4 (11)
Tail length	194.2 ± 14.9 (4)	190.7 ± 16.0 (3)	205.0 (1)	–	182.5 ± 7.6 (8)	226.1 ± 23.7 (10)
Outer rectrix width	24.2 ± 2.2 (4)	24.2 ± 2.2 (4)	–	–	24.3 ± 2.8 (7)	28.1 ± 4.6 (9)
Inner rectrix width	38.5 ± 1.9 (4)	38.0 ± 2.0 (3)	40.0 (1)	–	35.1 ± 3.9 (8)	41.8 ± 3.1 (10)
Tail graduation	97.3 ± 4.7 (3)	95.5 ± 4.9 (2)	101.0 (1)	–	90.7 ± 7.2 (5)	132.4 ± 26.1 (8)
Uppertail coverts greatest width	32.5 ± 3.3 (4)	31.3 ± 2.9 (3)	36.0 (1)	-	32.0 ± 2.8 (4)	37.2 ± 3.8 (10)

mined by analysing the PCR products with an ABI 373 A automated sequencer, and the software Genecan 3.7 and Genotyper 2.1.

RESULTS AND DISCUSSION

Mensural analyses

For most measurements, adult *L. imperialis* specimens (including known hybrids and the 1990 bird from near Cat Bin) were intermediate in size between adult *L. nycthemera* and *L. edwardsi* specimens of the same sex (Table 2). Crest length was highly variable among adult *L. imperialis* specimens, including those of the original series and even more so among known hybrids. Outer primary length did not conform well to the pattern of intermediacy among *L. imperialis* specimens, but the sample size for this character was very small. Except for the Cat Bin bird (see following), no specimen of *L. imperialis* showed mensural characters that would not be expected of hybrids between *L. nycthemera* and *L. edwardsi*.

The Cat Bin bird had an exceptionally long crest (Table 2), longer even than the mean for adult male *L. nycthemera*, and much longer than any other *L. imperialis*; this feature was clearly shown in the photographs. The Cat Bin bird also had long wings and tail, both similar to the mean for adult male *L. nycthemera* and much longer than any other *L. imperialis*. Its tarsus length was much longer than that of any specimen of *L. nycthemera*; differences in measurement technique probably explain this last anomaly (the Cat Bin specimen was measured by J. Eames). We were unable to measure any specimens of *L. hatinhensis*, but this species appeared (to P.R.) to be somewhat lankier and less chicken-like in shape compared with *L. edwardsi*. If this impression is borne out by measurements, it might explain why the Cat Bin *L. imperialis* was closer to *L. nycthemera* in some of its measurements, although the possibility of its being a backcross to *L. nycthemera* might provide an alternative or additional explanation.

PCA (Table 3, Fig. 1) confirmed the intermediacy of *L. imperialis* (except for the Cat Bin bird). In the PCA model used, by far the greatest amount of variance was explained on PC-I, a very strong size axis on which all characters had strongly positive loadings. PC-II showed a relatively weak contrast between culmen length and crest length. Other axes were even weaker and clearly not significant. Thus, for characters included in the PCA, overall size was the main quantitative difference between *L. edwardsi* and *L. nycthemera*, and loadings for *L. imperialis* specimens (including known hybrids) were largely intermediate between these two species, with scores for a few individuals overlapping with *L. edwardsi*, and the Cat Bin bird overlapping with *L. nycthemera*.

Table 3. Results from principal components analysis (graphed in Fig. 1) of adult *Lophura imperialis*, *L. edwardsi*, and Vietnamese races of *L. nycthemera*

Character	PC-I	PC-II
Culmen l from nares	0.70	–0.68
Crest l	0.79	0.37
Wing l (flattened)	0.89	0.01
Tarsus l	0.84	0.05
Tail l	0.87	0.16
Eigenvalues	3.37	0.63
Percent total variance explained	67.46	12.62

The sexes were included in the same analysis but were graphed separately on Fig. 1 for clarity.

Plumage analyses

All specimens of *L. imperialis* exhibited plumage characters that were to some degree intermediate between *L. edwardsi* and Vietnamese races of *L. nycthemera* (Appendix). Adult male *L. imperialis* of the original series (and most of the known hybrids) were generally glossy blue-black overall with moderately scalloped rear upperparts and greenish-tinged wing coverts; their crests varied from entirely blue-black to slightly or extensively mixed or barred with white, and while crest length varied greatly among adult male *L. imperialis*, most specimens had a wispy, thin crest. They were always much less glossy and less blue compared with adult male *L. edwardsi*, with much less prominently scalloped rear upperparts, and much less green-tinged wing coverts. Their crests never contained as much white as adult male *L. edwardsi*, nor were they as short and bushy. Compared with adult male *L. nycthemera*, adult male *L. imperialis* of the original series totally lacked any trace of the black-and-white patterning of the upperparts, highly variable in but clearly present in all races of the former species. Below, adult male *L. imperialis* showed glossy black underparts comparable to those of *L. nycthemera*, but their side feathers were much less lanceolate than in adult male *L. nycthemera*, and more so than in *L. edwardsi* (Appendix). The crest of adult male *L. imperialis* was much shorter and much less full than that of *L. nycthemera*, and unlike the latter species was not always entirely black. The tail of adult male *L. imperialis* was intermediate in length and degree of curvature between *L. edwardsi* and *L. nycthemera*, and while it was usually solid black like *L. edwardsi*, one specimen (CAS 60752) had a finely black-and-white barred tail, and the description of the original male (not preserved) indicates that it had faint chestnut spotting on the back and central rectrices (see below).

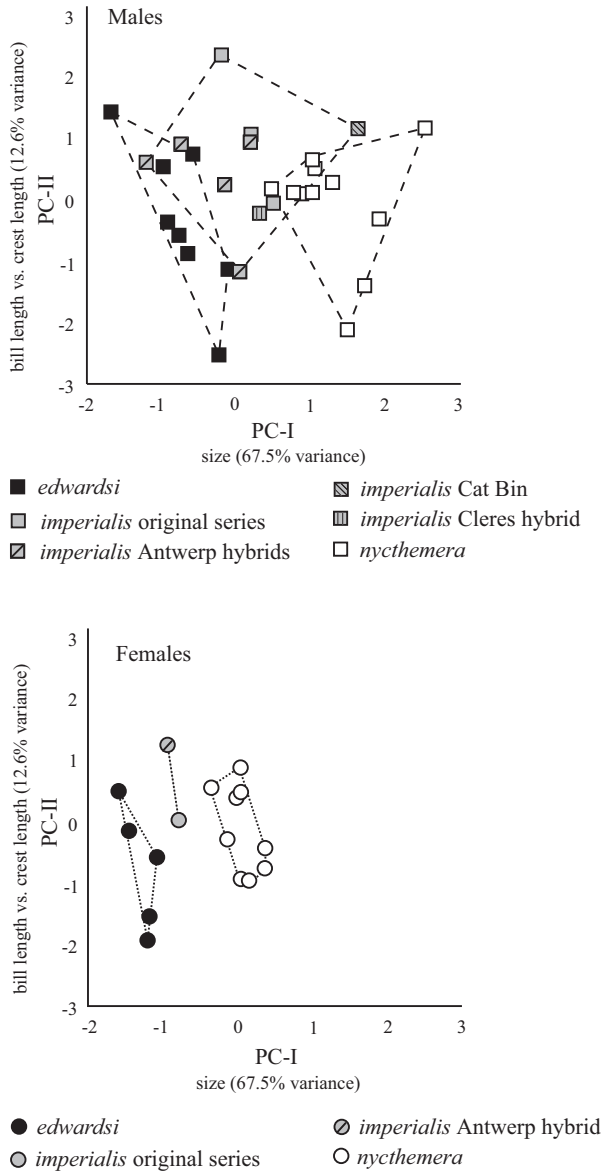

Figure 1. Graphs of results of principal components analysis of *Lophura imperialis*, *L. edwardsi*, and Vietnamese races of *L. nycthemera*. The sexes were included in the same analysis (see Table 3) but are graphed separately here for clarity.

Adult female *L. imperialis* of the original series (and the few known hybrids) showed variability and intermediacy in each of the several plumage characters that distinguished adult female *L. edwardsi* from adult females of Vietnamese races of *L. nycthemera* (Appendix). These included the colour and degree of shaft-streaking of head and body plumage (darker and warmer-toned, with very weak shaft-streaking in *L. edwardsi*; paler and greyer, with more shaft-streaking in *L. nycthemera*), the intermediate length of the crest, and the shape and distribution of blackish and chestnut in the tail. No plumage characters were observed among adult female *L. imperialis* that were not intermediate between the two putative parental species.

Among other age/sex classes of *L. imperialis*, the same situation was apparent (Appendix): each age/sex class of *L. imperialis* showed only plumage characters intermediate between those of *L. edwardsi* and *L. nycthemera*, or in a few cases they were shared with one of the latter two. Briefly, subadult male *L. imperialis* showed a muted *L. nycthemera*-type pattern in the central rectrices, whether the ground colour was white, buff, or chestnut. Subadult female and juveniles of both sexes of *L. imperialis* typically showed a more chestnut colour on the upperparts compared with the adults (as in subadult *L. edwardsi*) and some dark, pale-tipped markings on wing coverts. Downy young and birds in first contour plumage (still with downy heads) showed generally intermediate head markings, although further study is needed of the variation within downy *L. nycthemera*.

Thus, the strong and repeating pattern both in mensural and plumage characters was that *L. imperialis* of all ages and sexes were intermediate between the two putative parental species (without ruling out *L. hatinhensis* which was extremely similar to *L. edwardsi* except for the white central rectrices), and they exhibited no unique external morphological characters. This is clearly consistent with the hypothesis of a hybrid origin, and provides no support for the status of *L. imperialis* as a distinct species.

The fact that adult male *L. imperialis* showed none of the obvious species-specific plumage characters of *L. nycthemera* probably explains why its hybrid origin had not been suspected previously. Also, female *L. imperialis* did not show distinctive characteristics of the more familiar Chinese races of *L. nycthemera*, further contributing to the long-unquestioned status of *L. imperialis* as a full species. Instead, in male *L. imperialis* these obvious *L. nycthemera* characters were masked by the black overall colour of one of the parental species, and the tail and crest ornamentation of one parental species was reduced. This pattern is typical of numerous other crosses among *Lophura* and other pheasant species in which adult males of one parental species are generally black (P.R. unpubl. data). In contrast to males, female *L. imperialis* showed complete intermediacy, and species-specific characters were not masked by black coloration.

Experimental cross-breeding

Delacour described *L. imperialis* as follows (Delacour & Jabouille, 1924).

Adult male

'General colour of the male dark shining blue, with bright blue markings on the wing-coverts, back, rump, and upper tail-coverts; crest moderate and black; tail rather long and slightly curved. The feathers on the middle back and the two central tail-feathers faintly spotted with reddish-brown. Iris yellowish-brown; skin of the face bright scarlet; legs and feet crimson, spurs white; bill pale green, darker on the base of the upper mandible.

Wing 252 mm; tail 300 mm; culmen 30 mm; tarsus 86 mm.'

Adult female

'The adult female is bright chestnut on the back, wings, and upper and lower tail-coverts; head and neck pale brown, with cheeks and throat greyish-buff; primaries black, suffused with pale grey; secondaries chestnut, spotted and bordered with black; two central tail feathers chestnut-brown, marked with fine black spots and streaks, the others being black. All the brown and chestnut feathers are faintly spotted and streaked with black.

Wing 214 mm; tarsus 67 mm; tail 214 mm; culmen 28 mm.'

The phenotypes of the hybrids described below have been referenced according to their ring number. They differed from *L. imperialis* types in the following features.

Male N°317

Feathers of the back dark blue with reddish-brown fringes. Upper back and wing coverts black spotted with brown and white. Lower neck inconspicuously spotted with whitish feathers. Central pair of rectrices chestnut spotted with blackish. Second pair of rectrices black spotted with brown and white. Wing dark blue vermiculated with black and reddish brown.

Wing 255 mm; tarsus 86 mm; tail broken; culmen 31 mm.

Male N°334

Crest dark blue with the base black, some feathers faintly spotted with white. Back and wings black inconspicuously spotted with brown. The inner border of the second pair of tail feathers faintly spotted brown and white.

Wing 254 mm; tarsus 86 mm; tail 314 mm; culmen 30 mm.

Male N°321

Feathers of the wing coverts black with a dark metallic turquoise blue border. Lower part of the neck with a few shafts vermiculated white. Crest dark blue with the lower part black and a few feathers vermiculated with white on the base of the shaft.

Wing 258 mm; tarsus 86 mm; tail 340 mm; culmen 30 mm.

The bill of these three males was pale yellowish green and darker on the base of the upper mandible.

When 1 year old, the hybrid males differed from subadult *L. imperialis* in having the two central tail feathers dark blue, more strongly vermiculated with white and chestnut, the second pair of rectrices chestnut brown vermiculated with black and the third pair blue faintly vermiculated with chestnut on the inner border.

Female N°329

Underparts more olive-brown than chestnut. Central pair of rectrices dark brown marked with chestnut spots and streaks. The other rectrices dark brown with chestnut vermiculations becoming obsolete on the external tail feathers. Wing feathers dark brown vermiculated and streaked with chestnut.

Wing 232 mm; tarsus 69 mm; tail 226 mm; culmen 28 mm.

With regard to comparative measurements, the three males came close to *L. imperialis* with the exception of the tail of male N°321, which was slightly longer. The only female differed slightly in being of a larger size.

The tail of the males was long, pointed, and slightly curved with the central pair longer than the other rectrices, like *L. imperialis*. The crests and the general colour of these hybrids were excellent despite a slightly longer crest for male N°321. The mantle of males was dark blue, the body feathers being black with a blue fringe and the green gloss being absent from the wing coverts even though male N°321 exhibited a dark turquoise blue sheen. The colour of the facial skin, legs, feet, spurs and bills were like that of *L. imperialis*. The general colour of the female was more olive brown than the female syntype but such a colour was noted amongst the female progeny of the original pair.

Male hybrid N°317 differed from its brothers in the red brown fringe of the back feathers, the upper back and the wing coverts spotted with reddish brown and white, the wing feathers spotted chestnut and the two central tail feathers chestnut. In these features it resembled the specimen trapped on 27th February 2000 in Da Krong district.

Males N°317 and N°321 showed scarce white marks at the base of the neck. Such a character was shown by some descendants from the original pair and also by the 1990 Cat Bin specimen. The inconspicuously barred crest of males N°334 and N°321 was also observed on museum skins and noted by Delacour himself (Delacour & Jabouille, 1931).

The tail of the female differed likewise from the syntype in the mixed black and chestnut feathers but one F1 female kept in BMNH also exhibited this plumage anomaly (N°1948.70.1).

The tail pattern, with strong whitish or pale vermiculations on the two central feathers and even on the second pair for males N°317 and N°334, represents the main difference between the F1 male hybrids and the type description of male *L. imperialis*. Although not observed on the adult male museum skins, this character was also noted on the two central tail feathers of the 1990 specimen.

The more prominent whitish or pale spots on the males' central tail feathers may have resulted from the *L. nycthemera* subspecies which we selected for this experimental cross-breeding. Six subspecies of *L. nycthemera* occur in Vietnam, of which three overlap the range of *L. edwardsi* or *L. hatinhensis*: *L. n. beaulieui*, in Ha Tinh Province; Berlioz's silver pheasant *L. n. berliozi* in the western slopes of the Annamitic chain in Quang Tri and Quang Binh Provinces; Bel's silver pheasant *L. n. beli* on the ridges of the eastern slopes of the Annamitic chain in central Annam. There is a great deal of individual variation but the amount of black in the plumage increases from the north to the south (Delacour, 1948; McGowan & Panchen, 1994) resulting in much darker southern forms and two 'black' *L. nycthemera*, as can be observed in *L. n. annamensis* in Vietnam and *L. n. lewisi* in Cambodia (Delacour, 1948). *Lophura nycthemera beaulieui* is a lighter form closely related to the true silver pheasant *L. n. nycthemera*, the whitest subspecies; *L. n. berliozi* is intermediate between *beaulieui* and *beli* and is a rather unstable form showing a great deal of individual variation (Delacour, 1948); *L. n. beli* is the darkest of the three subspecies. A crossing between one of these subspecies and *L. edwardsi* may result in a variable amount of white in the hybrid's plumage, the darker phenotypes being obtained with *L. n. beli*. Furthermore the male of *L. n. berliozi* which we used for this experiment was a whitish individual that may have been itself the result of a past cross-breeding with *L. n. nycthemera* (S. Moulin, unpubl. data), which therefore induced whitish spots on the tail not typical of *L. imperialis*. Unfortunately there is no captive population of the rare *L. n. beli* and only this one male *L. n. berliozi* was available to us for the experimental cross-breeding.

Alternatively, the pale vermiculations on the central feathers may be characteristic of a first hybrid generation, which would be erased by a backcross to *L. edwardsi* or breeding between a pairing of siblings. No attempt was made to backcross our hybrids to *L. edwardsi* but we paired male N°321 with its sister and obtained one F2 male that looked quite like *L. imperialis*, differing only in having a few small white marks at the base of the neck when 1 year old. Furthermore such experiments were conducted by K. Wood using *L. edwardsi* and *L. diardi* (pers. comm.). The resultant offspring exhibited very little or no phenotypic variation. Males were inky violet blue and females closely resembled skins of AMNH *L. imperialis*, although a bit more russet. The problematic characters in the F1 generation disappeared in the backcross with *L. edwardsi*. Conversely, pairing of siblings from *L. diardi* × *L. edwardsi* produced more variable progeny, some of which resemble *L. imperialis*, despite purple or clear violet sheens, and others were similar to 'black' *L. nycthemera*. Therefore it seems that a backcross with *L. edwardsi* or the pairing of siblings may produce *L. imperialis* morphs exhibiting very little phenotypic variation (K. Wood, pers. comm.).

Genetic studies

The relationships of the *L. imperialis* mtDNA CR sequences with other species of *Lophura* are described by the neighbour-joining tree (Fig. 2). There were two kinds of sequences among *L. imperialis*: the first one was identical to homologue sequences from a sample of captive-reared and wild *L. edwardsi* and *L. hatinhensis*; the other one was related to the *L. nycthemera* sequences. These findings suggest that *L. imperialis* could have received mtDNA from *L. edwardsi*/*L. hatinhensis* females or from populations closely related to *L. nycthemera*. The neighbour-joining tree represented in Figure 2 is based on *c.* 184 nucleotides only, because the museum samples of *L. imperialis* did not allow sequencing of longer parts of the mtDNA CR. Analyses of microsatellite allele size in species of *Lophura* are reported in Table 4. It is noteworthy that samples of *L. imperialis* had no unique alleles at any locus. Samples attributed to *L. imperialis* shared alleles with *L. edwardsi*, *L. hatinhensis* and *L. nycthemera* at loci M1, M2 and M4, and did not show unique alleles or alleles shared with *L. leucomelana* and *L. swinhoei* at loci M1 and M2. Therefore, it is probable that *L. imperialis* originated from the crossing of *L. edwardsi*, *L. hatinhensis* and *L. nycthemera.*

CONCLUSION

Lophura imperialis showed no unique plumage or shape features. Indeed, there was no consistent phenotype, and each individual showed plumage anomalies also exhibited by known hybrids. Morphological data thus strongly support the hybrid origin of *L. imperialis*, involving *L. edwardsi* and *L. nycthemera* as the parents (Fig. 3).

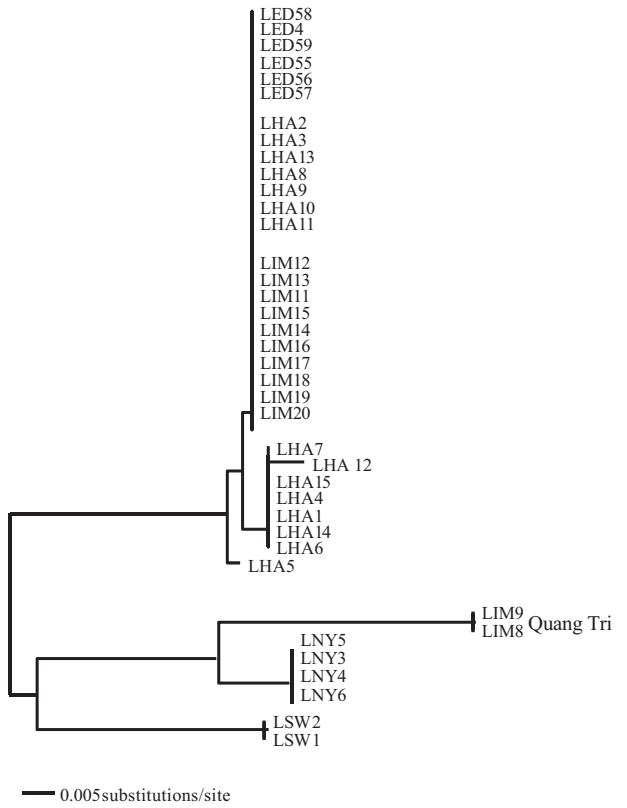

Figure 2. Neighbour-joining tree (based on *c.* 184 nucleotides only; see text) showing phylogenetic relationships of the sequenced mitochondrial DNA control regions of the three endemic *Lophura* species, *L. n. nycthemera* and *L. swinhoei*. (LED, *L. edwardsi*; LHA, *L. hatinhensis*; LIM, *L. imperialis*; LNY, *L. n. nycthemera*; LSW, *L. swinhoei*).

The experimental cross-breeding of *L. n. berliozi* × *L. edwardsi* strongly support the museum studies and the hybrid origin of *L. imperialis*. Two of three hybrid males were very like the type description of *L. imperialis*, and the third closely resembled the bird trapped in Da Krong Province in early 2000. Most of the plumage anomalies shown by the Clères hybrids were also exhibited by museum specimens, even the pale spots on the central tail feathers that occurred on the 1990 specimen. Nevertheless the male *L. imperialis* described as the type may not be a hybrid of first generation but the result of a backcross to *L. edwardsi* or of a pairing of hybrids of the first generation.

Gene analyses confirmed the morphological data and the hybrid origin of *L. imperialis*. All mtDNA sequences from museum skins were identical to *L. edwardsi* sequences, whilst that of the 2000 trapped bird grouped with the *L. nycthemera* clade. Microsatellites were identical to those of *L. edwardsi* or a combination of *L. edwardsi* and *L. nycthemera*.

Thus there is overwhelming evidence to conclude that *L. imperialis* is a natural hybrid and as such it should be removed from taxonomic lists, as well as lists of species of conservation concern.

On the basis of the geography as well as morphology and genetic analyses, the putative parental taxa for the original pair would be *L. n. beli* × *L. edwardsi,* whilst that of the 2000 bird would be *L. edwardsi* × *L. n. beli.* The putative parental taxa of the 1990 bird are more enigmatic as *L. edwardsi* does not occur in Ha Tinh province, where it is replaced by *L. hatinhensis*. This taxon differs from *L. edwardsi* only by having several variable and asymmetrical white tail feathers. Recent morphological and genetic

Table 4. Molecular size of alleles at studied microsatellite loci in samples of *Lophura*

Species	M1	M2	M3	M4	M5	M6	M7	M8	M9
L. edwardsi	206, 208, 214, 216, 218, 228	294, 295, 297, 299	214, 216, 218, 220	146, 148	284	113, 114, 115, 116	171, 173	258, 274, 276	255, 257
L. hatinhensis	206, 214	278, 295, 296, 297	214, 216, 218, 220	146	284	111, 113, 114	169, 171, 173	258, 276	255, 257, 259
L. leucomelana	210, 220, 228	297	214, 218	148	276, 284	–	–	–	–
L. nycthemera	210, 214, 218, 220, 222, 224, 228, 232	297, 299	216, 218	146, 148	276, 284	113, 114, 115	171	276	255, 257, 263
L. swinhoei	200, 204	294	218	–	276, 283	–	171	–	–
L. imperialis	214, 218	295, 299	214, 218	146	276, 284	–	–	–	–

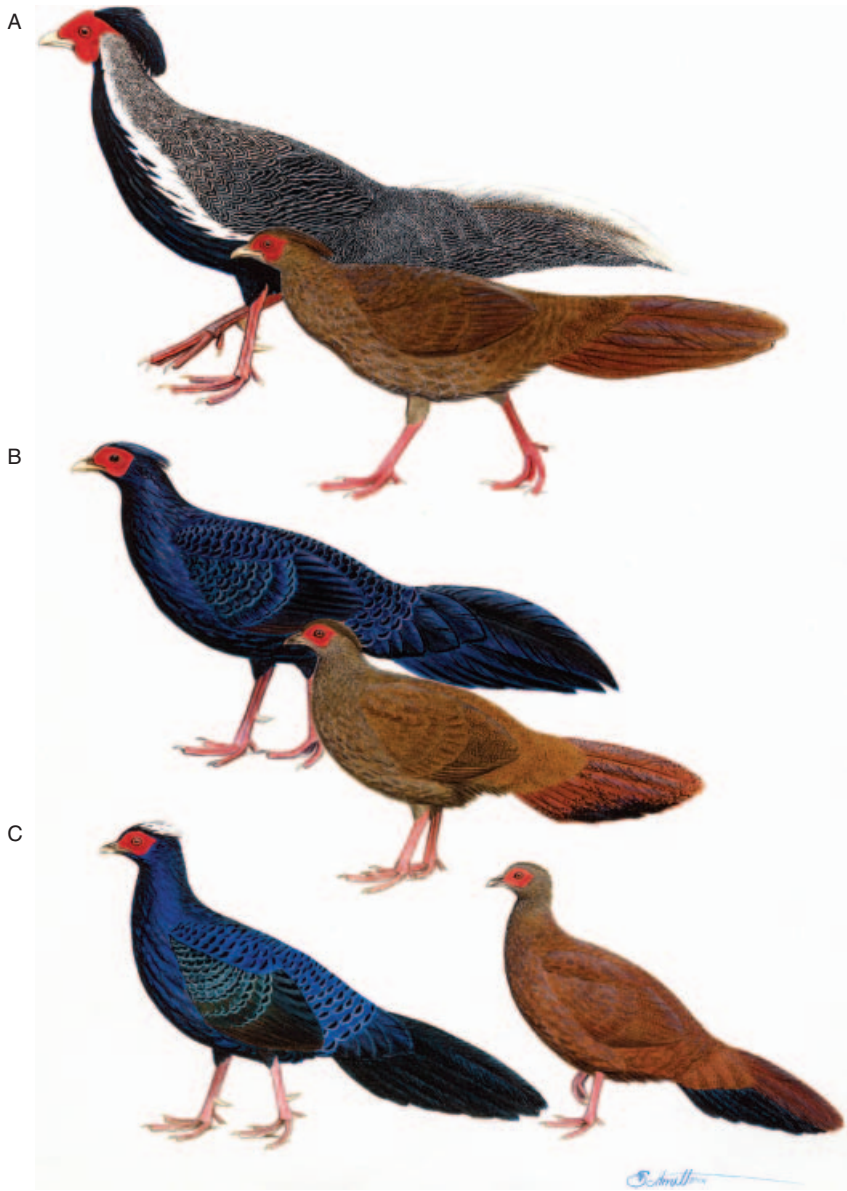

Figure 3. *Lophura imperialis* (B) between its parental species, *L. nycthemera* (A) and *L. edwardsi* (C). Painting by John Schmitt.

studies suggest it may just be an inbred form of *L. edwardsi* (A. Hennache & E. Randi, unpubl. data). Therefore its crossing with *L. nycthemera* would result in phenotypes also resembling *L. imperialis*, and the putative parental taxa for the 1990 specimen would be *L. n. beaulieui* × *L. hatinhensis.*

Conservation implications

Hybridization usually occurs in contact zones or in continuous zones where characters are graded clinally from one taxon to another. Anthropogenic modifications of natural habitats, such as fragmentation, can also result in hybridization. In these isolated pockets species may hybridize more than they do under more natural conditions, due to the rarity of mates of their own species (Dowling & Secor, 1997). *Lophura edwardsi* is a very rare species, so much so that it was even for a time thought to be extinct in the wild; it is now restricted to small patches of primary or secondary evergreen forest, while *L. nycthemera* is a generalist species that may tolerate a much wider habitat range. *Lophura hatinhensis* is also very rare and was only recently brought to the attention of science. Today, massive deforestation has resulted in forest fragments where these taxa may cohabit and

sometimes mate. Thus the fragmented habitat might induce introgressive hybridization from *L. nycthemera* into the wild *L. edwardsi* and *L. hatinhensis* populations, of which the birds trapped in 1990 and 2000 are manifestations. Alternatively, it is noteworthy that *L. nycthemera* and *L. edwardsi* are sympatric, and it is possible that low levels of hybridization may be natural between these species, though they do not usually share the same habitat.

Hybridization and introgression could introduce genetic variation and reduce inbreeding depression in the small population size (Grant & Grant, 1994). Positive consequences include a genetic enrichment of the endangered form when the hybrids backcross (Arnold *et al*., 1999) and greater fitness in a fluctuating environment (Grant & Grant, 1994). Negative consequences concern the conservation of the rarest taxa *L. edwardsi* and *L. hatinhensis*. In the smallest isolated forest fragments, populations may evolve combinations of characters inherited from the two parental taxa and attain evolutionary independence (Dowling & Secor, 1997) of which *L. imperialis* might be one manifestation.

ACKNOWLEDGEMENTS

We are grateful to Kermit Wood (Pleistocene Zoological Trust, USA) for sharing information about the backcross of F1 hybrids with *L. edwardsi*, Professor Vo Quy (CRES, Hanoi) and Jonathan Eames (BirdLife Vietnam) for providing us with descriptions, samples and pictures of the 2000 trapped bird, Truong Van La (IEBR, Hanoi) and Dang Gia Tung (Hanoi Zoo) for their assistance at Hanoi in helping us to check the 1990 trapped bird, Robert Prys-Jones (BMNH) and Claire and Jean-François Voisin (MNHN) who provided us with museum samples, Nigel Collar for suggesting that P.R. study this problem and for checking label data at the MNHN, and Michel Saint Jalme (MNHN) who kindly set up the artificial insemination of an *L. edwardsi* female with semen from *L. n. berliozi*. We thank the staff of the following institutions for providing access to specimen material: American Museum of Natural History, New York (AMNH), California Academy of Sciences, San Francisco (CAS), Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ), Museum National d'Histoire Naturelle, Paris, France (MNHN), Royal Ontario Museum, Toronto (ROM), University of Michigan Museum of Zoology, Ann Arbor (UMMZ), National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), Peabody Museum, Yale University, New Haven (YPM), Zoologisches Museum, Berlin (ZMB). Staff of the Antwerp Zoo allowed P.R. to examine specimens of the captive hybrid population kept frozen there. Funding was provided by the Museum National d'Histoire Naturelle, the Smithsonian Institution, and the Istituto Nazionale per la Fauna Selvatica (INFS), Bologna, Italy.

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APPENDIX

Selected plumage characters for each specimen of *Lophura imperialis* and the putative parental species (*L. edwardsi*, *L. hatinhensis*, and Vietnamese races of *L. nycthemera*). Label data on origin of specimen is in quotes where reproduced verbatim. See Acknowledgements for explanation of museum acronyms.

Table A. Adult males (1)

			Character					
Species	Specimen bird no	Origin	Crest colour	Crest length	Neck/mantle colour	Scapulars/rump feathers	Wing coverts	Breast colour
edwardsi			white	short	smooth, very glossy blue	strongly scalloped, very glossy blue	strongly scalloped, very glossy green	smooth, glossy blue
hatinhensis			white	short	smooth, very glossy blue	strongly scalloped, very glossy blue	strongly scalloped, very glossy green	smooth, glossy blue
imperialis	MNHN 1934.1388	'né et mort en captivité à Clères'	black, whitish bases	mid-length	smooth, glossy blue	moderately scalloped, glossy blue	moderately scalloped, greenish-blue	not recorded
imperialis	MNHN 1936.1548	'mort à Clères, issu de parents originaires d'Annam . . . , 15 avril 1936'	black, whitish bases	mid-length	smooth, glossy blue	moderately scalloped, glossy blue	moderately scalloped, greenish-blue	not recorded
imperialis	BMNH 1931.5.11.5	'issued from wild birds . . .'	barred black and white	mid-length	smooth, glossy blue-black	moderately scalloped, glossy blue	moderately scalloped, greenish-blue	smooth, glossy blue-black
imperialis	CAS 60752	died 1947	black	mid-length	smooth, glossy blue-black	moderately scalloped, glossy blue	no green tinge	glossy blue-black, white-shafted
imperialis	AMNH 648214	'Rec'd 1956' 'received from Wm. J. MacKenson by Jean Delacour...'	greenish-black	rather long	smooth, glossy blue-black	moderately scalloped, glossy blue	moderately scalloped, greenish-blue	smooth, glossy blue-black
imperialis	mount	Antwerp hybrid	blue-black	rather long	smooth, glossy blue-black	moderately scalloped, glossy blue	moderately scalloped, greenish-blue	smooth, glossy blue-black
imperialis	352/75	Antwerp hybrid; 'keiserfasant'; 16-6-75	blue-black	rather long	smooth, glossy blue-black	moderately scalloped, glossy blue	moderately scalloped, greenish-blue	smooth, glossy blue-black
imperialis	590/76	Antwerp hybrid; 'keiser x zilver'; 29-9-76	blue-black	mid-length	smooth, glossy blue-black	moderately scalloped, very glossy blue	moderately scalloped, very glossy greenish-blue	smooth, glossy blue-black
imperialis	651/74	Antwerp hybrid; 'zilver x keiser'	blue-black	moderate	smooth, glossy blue-black	moderately scalloped, glossy blue	moderately scalloped, greenish-blue	smooth, blue-black

Table A. *Continued*

Species	Specimen bird no	Origin	Character					
			Crest colour	Crest length	Neck/mantle colour	Scapulars/rump feathers	Wing coverts	Breast colour
imperialis	342/82	Antwerp hybrid; 'keiserfasant'; 27-7-82	black with much white at base	moderate	smooth, glossy blue-black	strongly scalloped, very glossy blue	strongly scalloped, very glossy green	not recorded
imperialis	720/75	Antwerp hybrid; 'keiserfasant'; 24-12-75	black	long	smooth, glossy blue-black	moderately scalloped, glossy blue	moderately scalloped, greenish-blue	smooth, glossy blue-black
imperialis	64	Antwerp hybrid; 'bastaard keiserfasant'; 26/2/88	blue-black	rather long	smooth, glossy blue-black; white speckles on sides of head and neck	moderately scalloped, blue and copper-tinged	blackish, copper-tinged	glossy blue-black, strong white shaft streaks on sides
imperialis	701/76	Antwerp hybrid; 'keiser x zilver'; 2-2-76	blue-black	very long	smooth,	moderately scalloped, glossy blue-black; white speckles on sides of head and neck	moderately scalloped, glossy blue, rump copper-tinged	glossy blue greenish-blue
nycthemera (*annamensis, beli, berliozi*)			black	long	finely to coarsely vermiculated black-white	finely to coarsely vermiculated black-white	finely to coarsely vermiculated black-white	slightly glossed blue-black

Table B. Adult males (2)

Species	Specimen bird no	Origin	Character					
			Side feather shape	Undertail coverts colour	Mid-belly colour	Central rectrices	Outer rectrices	Tail shape
edwardsi			rounded, not elongate	scalloped, glossy blue	unglossed blackish	glossy blue-black	glossy blue-black	vaulted, uncurved, rather short
hatinhensis			rounded, not elongate	scalloped, glossy blue	unglossed blackish	white	glossy blue-black	vaulted, uncurved, rather short
imperialis	MNHN 1934.1388	'né et mort en captivité à Clères'	triangular	slightly scalloped blue-black	slaty blackish	bluish-black	blue-black	vaulted, slightly curved, mid-length

imperialis	MNHN 1936.1548	'mort à Clères, issu de parents originaires d'Annam . . ., 15 avril 1936'	triangular	slightly scalloped blue-black	slaty blackish	bluish-black	blue-black	vaulted, slightly curved, mid-length
imperialis	BMNH 1931.5.11.5	'issued from wild birds . . .'	triangular	slightly scalloped	black blue-black	bluish-black	blue-black	vaulted, slightly curved, mid-length
imperialis	CAS 60752	died 1947	not recorded	not recorded	not recorded	finely barred white and black	not recorded	not recorded
imperialis	AMNH 648214	'Rec'd 1956' 'received from Wm. J. MacKenson by Jean Delacour . . .'	slightly elongate, triangular-tipped	slightly scalloped blue-black	unglossed blackish	bluish-black	blue-black	vaulted, slightly curved, mid-length
imperialis	mount	Antwerp hybrid	slightly elongate, triangular-tipped	not recorded	unglossed blackish	bluish-black	not recorded	vaulted, slightly curved, mid-length
imperialis	352/75	Antwerp hybrid; 'keiserfasant'; 16-6-75	slightly elongate, triangular-tipped	not recorded	unglossed blackish	bluish-black	blue-black	vaulted, mid-length (bent in storage)
imperialis	590/76	Antwerp hybrid; 'keiser × zilver'; 29-9-76	elongate, lanceolate	slightly scalloped blue-black	unglossed blackish	bluish-black	blue-black	vaulted, mid-length (bent in storage)
imperialis	651/74	Antwerp hybrid; 'zilver × keiser'	slightly elongate, triangular-tipped	scalloped blue-black	unglossed blackish	bluish-black	blue-black	poorly preserved
imperialis	342/82	Antwerp hybrid; 'keiserfasant'; 27-7-82	not recorded	slightly scalloped blue-black	not recorded	bluish-black	blue-black	vaulted, mid-length (bent in storage)
imperialis	720/75	Antwerp hybrid; 'keiserfasant'; 24-12-75	slightly elongate, triangular-tipped	not recorded	unglossed blackish	bluish-black	blue-black	poorly preserved
imperialis	64	Antwerp hybrid; 'bastaard keiserfasant'; 26/2/88	slightly elongate, triangular-tipped	not recorded	not recorded	not recorded	not recorded	not recorded
imperialis	701/76	Antwerp hybrid; 'keiser × zilver'; 2-2-76	elongate, lanceolate	not recorded	unglossed blackish	bluish-black	blue-black	vaulted, mid-length (bent in storage)
nycthemera (*annamensis*, *beli*, *berliozi*)			lanceolate	slightly glossed blue-black	unglossed blackish	almost solid white to vermiculated black-white	finely to coarsely vermiculated black-white	vaulted, curved, rather long

Table C. Adult females (1)

Species	Specimen bird no	Origin	Character					
			Crest colour	Crest length	Neck/mantle colour	Scapulars/rump feathers	Wing coverts	Breast colour
edwardsi			grey-brown	very short	uniform dark grey-brown	uniform rufous-brown	uniform rufous-brown	uniform grey-brown
hatinhensis			grey-brown	very short	uniform dark grey-brown	uniform rufous-brown	uniform rufous-brown	uniform grey-brown
imperialis	MNHN 1934.1389	'né et mort en captivité à Clères'	dark grey-brown	short	dark neutral brown dark (fresh)	rufous-brown (fresh)	dark rufous-brown (fresh)	weakly shaft-streaked grey-brown
imperialis	MNHN 1928.1117	'mort à Clères, le 18 September 27' 'cotype'	pale brown (worn)	short	blotchy neutral brown (worn)	blotchy warm brown (worn)	blotchy pale and rufous-brown (worn)	blotchy, pale neutral brown
imperialis	BMNH 1948.70.1	'de Clères'	neutral brown	rather short	slightly shaft-streaked neutral brown	slightly shaft-streaked warm brown	slightly shaft-streaked warm brown	shaft-streaked olive-brown
imperialis	AMNH 648215	'Rec'd 1956' 'received from Wm. J. MacKenson by Jean Delacour . . .'	neutral brown	mid-length	very finely vermiculated, shaft-streaked grey-brown	very finely vermiculated, shaft-streaked rufous-brown	very finely vermiculated, shaft-streaked rufous-brown	very finely vermiculated, shaft-streaked rufous-brown
imperialis	739/75	Antwerp hybrid; 'kaiser fasant', '30–12–75'	neutral brown	mid-length	slightly shaft-streaked neutral brown	slightly shaft-streaked rufous brown	slightly shaft-streaked rufous brown	shaft-streaked olive-brown
nycthemera (*annamensis*, *beli*, *berliozi*)			dark grey-brown	rather long	shaft-streaked pale grey-brown to olive-brown	shaft-streaked olive-brown	shaft-streaked olive-brown	shaft-streaked olive-brown

Table D. Adult females (2)

Species	Specimen bird no	Origin	Character					
			Side feather shape	Undertail coverts colour	Mid-belly colour	Central rectrices	Outer rectrices	Tail shape
edwardsi			rounded, not elongate	broad rufous-brown tips, blackish bases	uniform grey-brown	very dark chestnut to slightly glossy blackish	slightly glossed black	vaulted, uncurved, rather short
hatinhensis			rounded, not elongate	probably as *edwardsi*	uniform grey-brown	white	slightly glossed black	vaulted, uncurved, rather short
imperialis	MNHN 1934.1389	'né et mort en captivité à Clères'	rounded triangles	dark rufous, darker bases	grey-brown	very frayed, grey-brown	finely black-speckled chestnut	very frayed
imperialis	MNHN 1928.1117	'mort à Clères, le 18 September 27' 'cotype'	rounded triangles	dark rufous, darker bases	grey-brown	blackish-chestnut	blackish-chestnut	vaulted, very little curved, mid-length
imperialis	BMNH 1948.70.1	'de Clères'	rounded triangles	black-speckled rufous-brown	grey-brown	very dark chestnut-brown	very dark chestnut with broad black tips	vaulted, very little curved, mid-length
imperialis	AMNH 648215	'Rec'd 1956', 'received from Wm. J. MacKenson by Jean Delacour . . .'	rounded triangles	rufous-brown-tipped blackish	dull brown	weakly rufous-vermiculated glossy blackish	glossy blackish	vaulted, very little curved, mid-length
imperialis	739/75	Antwerp hybrid; 'kaiser fasant', '30–12–75'	rounded triangles	black-speckled brown	neutral brown with blackish blotches	finely chestnut-vermiculated black	rufous-tinged blackish	vaulted, mid-length (bent in storage)
nycthemera (*annamensis*, *beli*, *berliozi*)			rather triangular	bright rufous-brown	pale grey-brown	dark chestnut-brown	dark chestnut-brown	vaulted, slightly curved, rather long

Table E. Subadult males (1)

Species	Specimen bird no	Origin	Character					
			Crest colour	Crest length	Neck/mantle colour	Scapulars/rump feathers	Wing coverts	Breast colour
edwardsi			barred black-and-white	short	sooty (old) and very glossy blue (new)	dusky, rufous-marked (old) and very glossy blue (new)	finely marked rufous (old) and very glossy, scalloped (new)	sooty (old) and glossy blue (new)
hatinhensis			whitish (details not recorded)	short	sooty (old) and very glossy blue (new)	dusky (old) and glossy blue (new)	dusky (old)	dusky (old) and glossy blue (new)
imperialis	MNHN 1931.144	'fils du couple original provenant . . .' 'Clères, né en captivité mai 1930, [died] 15 mars 1931'	blue-black	short	smooth, glossy blue-black	mixed rufous-brown (old) and scalloped blue-black (new)	mixed rufous-brown (old) and blackish (new)	blue-black
imperialis		Cat Bin	blue-black	long	glossy blue-black with some white speckling and shaft streaks	finely vermiculated and rufous-brown (old) blue-black (new)	finely vermiculated rufous-brown	slightly glossy blue-black with whitish shaft streaks
imperialis	312	Clères hybrid	neutral brown (old) and blue-black (new)	short	neutral brown (old) and blue-black with white speckling on neck sides	finely vermiculated and blue-black (new)	finely barred rufous-brown (old)	slightly glossy blue-black rufous-brown and black
imperialis	317	Clères hybrid	neutral brown (old) and blue-black (new)	rather short	neutral brown (old) and blue-black with white speckling on neck sides	finely vermiculated and blue-black (new)	finely barred rufous-brown (old)	slightly glossy blue-black rufous-brown and black
imperialis	321	Clères hybrid	blue-black	mid-length	neutral brown (old) and blue-black with white speckling on neck sides	finely vermiculated and blue-black (new)	rufous-brown (old) rufous-brown and black	finely barred glossy blue-black
imperialis	334	Clères hybrid	neutral brown (old) and blue-black (new)	short	neutral brown (old) and blue-black with white	finely vermiculated rufous-brown (old) speckling on neck sides	finely barred rufous-brown and black and blue-black (new)	slightly glossy blue-black
nycthemera berliozi		Clères	black-tipped	rather short	olive brown	olive brown	olive brown	strongly black-and-white barred, and black-blotched centrally

Table F. Subadult males (2)

Species	Specimen bird no	Origin	Character					
			Side feather shape	Undertail coverts colour	Mid-belly colour	Central rectrices	Outer rectrices	Tail shape
edwardsi			rounded	blackish, weakly blue-scalloped	sooty	blackish	blackish	vaulted, uncurved, rather short
hatinhensis			not recorded	not recorded	not recorded	blackish	blackish	vaulted, uncurved, rather short
imperialis	MNHN 1931.144	'fils du couple original provenant . . .' 'Clères, né en captivité mai 1930, [died] 15 mars 1931'	rounded triangles	not recorded	dull greyish-black	dusky bluish-black	not recorded	vaulted, slightly curved, mid-length
imperialis		Cat Bin	acute triangles (slightly lanceolate)	dusky black with broad whitish shaft streaks	dull brownish-black	blackish with strong rufous-buff vermiculation	dusky black	vaulted, slightly curved, rather long
imperialis	312	Clères hybrid	acute triangles (slightly lanceolate)	blue-black	unglossed black	finely black-and-white barred, tips rufescent	black with weak rufous barring on edging	vaulted, slightly curved, mid-length
imperialis	317	Clères hybrid	not recorded	not recorded	not recorded	missing	blackish	most feathers missing
imperialis	321	Clères hybrid	acute triangles (slightly lanceolate)	dusky black	unglossed black	finely black-and-white barred, tips rufescent	dusky black	vaulted, slightly curved, mid-length
imperialis	334	Clères hybrid	not recorded	not recorded	unglossed black	strongly black-and-white	blackish	damaged
nycthemera berliozi		Clères	strongly black-and-white barred	not recorded	not recorded	barred strongly black-and-white barred	strongly black-and-white barred	vaulted, uncurved, mid-length

Table G. Subadult females (1)

Species	Specimen bird no	Origin	Character					
			Crest colour	Crest length	Neck/mantle colour	Scapulars/rump feathers	Wing coverts	Breast colour
edwardsi			grey-brown	very short	neck grey-brown, mantle rufous-brown	rufous	rufous with buff and black speckles	shaft-streaked rufescent brown
*hatinhensis**			grey-brown	very short	dark brown	dark warm brown	dark warm brown	not recorded
imperialis	AMNH 388264	'born in captivity at Yardley, Pa. May 1951; died October 12, 1951'; '5th generation from the original pair . . .'	neutral brown	very short	finely vermiculated warm brown	finely vermiculated warm brown	finely vermiculated warm brown	shaft-streaked, finely vermiculated warm brown
imperialis	488/81	Antwerp hybrid; 'keiserfasant'; sex and age class not certain	brownish	rather short	finely vermiculated warm brown	finely vermiculated warm brown; rump feathers bluish-tipped	finely vermiculated warm brown with black blotches and whitish tips	shaft-streaked warm brown
imperialis	329	Clères hybrid	dark grey-brown	rather short	dark warm brown	dark warm brown	dark warm brown	shaft-streaked dark warm brown
nycthemera (*annamensis*, *beli*, *berliozi*)			dark brown	rather short	neutral to warm brown	neutral to warm brown	neutral to warm brown with buff and black speckles	shaft-streaked pale neutral to rufescent brown

*Not directly compared with *edwardsi*; further comparisons needed.

Table H. Subadult females (2)

Species	Specimen bird no	Origin	Character					
			Side feather shape	Undertail coverts colour	Mid-belly colour	Central rectrices	Outer rectrices	Tail shape
edwardsi			rounded	rufous-tipped blackish	brownish-grey	very dark chestnut	blackish with chestnut markings	vaulted, uncurved, rather short
*hatinhensis**			not recorded	not recorded	not recorded	blackish	blackish	vaulted, uncurved, rather short
imperialis	AMNH 388264	'born in captivity at Yardley, Pa. May 1951; died October 12, 1951'; '5th generation from the original pair'	rounded triangles	rufous-tipped blackish	brownish-grey	finely vermiculated buff, rufous, and blackish	blackish	vaulted, uncurved, rather short
imperialis	488/81	Antwerp hybrid; 'keiserfasant'; sex and age class not certain	not recorded	not recorded	not recorded	finely vermiculated buff, rufous, and blackish	blue-black	vaulted, slightly curved, mid-length
imperialis	329	Clères hybrid	rounded triangles	not recorded	not recorded	missing	coarsely barred rufous-brown and blackish	most feathers missing
nycthemera (*annamensis*, *beli*, *berliozi*)			not recorded	rufescent	pale grey-brown	finely marked chestnut	finely marked chestnut	vaulted, slightly curved, mid-length

*Not directly compared with *edwardsi*; further comparisons needed.

Table J. Juvenile males

Species	Specimen bird no	Origin	Character								
			Crown colour	Mantle colour	Scapulars	Wing coverts	Breast colour	Side feather shape	Mid-belly colour	Central rectrices	Outer rectrices
edwardsi			dark grey-brown	lightly black-speckled rich chestnut (old), very glossy blue (new)	dark-edged bright chestnut	bright chestnut with dark subterminal bands, buff tips	dark-speckled chestnut (old), glossy blue often with chestnut shaft streaks (new)	dark-speckled chestnut (old), glossy blue often with chestnut shaft streaks (new)	dusky grey	very dark chestnut to blue-black	blackish
imperialis	YPM 24660	'State Game Farm, Ithaca, N.Y.'; not yet full-sized	dark brown	scalloped black and chestnut	scapulars chestnut, tipped black; rump chestnut	chestnut with blue-black subterminal bands, buff tips	blackish with chestnut shaft streaks	rounded	dingy whitish	blackish	brownish-black
imperialis	BMNH 1926.9.9.3	'né à Clères en Mai 1926'; about half-grown	neutral brown	chestnut	chestnut	chestnut with blue-black subterminal bands, buff tips	warm brown with pale shaft streaks (old), blue-black (new)	not recorded	buffy and grey	very dark chestnut vermiculated black	blackish and chestnut
imperialis	MNHN 1927.2375	'4 août 1927'; not full-sized	dark brown	buff shaft-streaked dark warm brown	buff shaft-streaked dark warm brown	buff shaft-streaked dark warm brown, black subterminal spots and buff tips	buff shaft-streaked blackish	buff-tipped blackish	blackish-grey	bronzy-black	chestnut-and-black barred

Table K. Juvenile females

Species	Specimen bird no	Origin	Character								
			Crown colour	Mantle colour	Scapulars	Wing coverts	Breast colour	Side feather shape	Mid-belly colour	Central rectrices	Outer rectrices
edwardsi		not full-sized	dark brown	shaft-streaked, weakly vermiculated dark warm brown	shaft-streaked, weakly vermiculated dark warm brown	weakly vermiculated dark warm brown, blackish subterminal spots, buff tips	shaft-streaked dark warm brown	shaft-streaked dark warm brown	dark grey	very dark chestnut	not recorded
imperialis	MNHN 1927.2376	'jeune ? [male symbol], Don de M Delacour, 19 juillet 1927'; not full-sized	dark brown	shaft-streaked, weakly vermiculated neutral brown	shaft-streaked, weakly vermiculated neutral brown	weakly vermiculated neutral brown with a few blackish subterminal spots	shaft-streaked neutral brown	shaft-streaked neutral brown	weakly, finely barred dull brown	black-flecked dark chestnut	black-flecked dark chestnut
nycthemera (*annamensis*, *beli*, *berliozi*)		not full-sized	dark brown	finely vermiculated neutral brown	finely vermiculated neutral brown, some feathers with dark subterminal spots	finely vermiculated neutral brown with dark subterminal spots and buff tips	shaft-streaked neutral brown	shaft-streaked neutral brown	slightly barred greyish	dark chestnut	dark chestnut

Table M. First contour plumage (head still downy)

			Character								
Species	Specimen bird no	Origin	Crown pattern	Crown colour	Supercilium	Eye-stripe	Mantle colour	Scapulars	Wing coverts	Breast colour	Mid-belly colour
edwardsi		Clères 36 days	not recorded	dark brown	yellow-buff	strong blackish postocular stripe	not recorded	chestnut with large black subterminal spots	chestnut with large black subterminal spots and buff terminal streaks	boldly, irregularly barred and spotted black and chestnut	whitish
imperialis	BMNH 1930.6.12.2		strong black forehead streak	pale tawny	rufous-buff postocular stripe	strong blackish finely vermiculated	pale shaft-streaked, and pale-tipped, warm brown	pale shaft-streaked and blackish-tipped, finely vermiculated warm brown	pale shaft-streaked warm brown finely vermiculated warm brown	pale shaft-streaked	pale grey-brown
imperialis	MNHN 1926.239	'poussin, Haut-Annam, né et mort en captivité à Clères'	not recorded	dark brown	rufous-buff	fairly strong blackish postocular streak	dark chestnut with prominent buff streaks	dark chestnut with prominent buff streaks and black spots	dark chestnut with prominent buff streaks and dark tips	blackish with chestnut bars and rufous shaft streaks	pale grey-brown
imperialis	MNHN 1917.2374	'poussin né et mort en captivité à Clères'	not recorded	dark brown	pale buff	weak dark postocular streak	dark chestnut with weak buff streaks	dark chestnut with weak buff streaks	dark chestnut with dark subterminal spots and narrow pale tips	dark warm brown with pale shaft streaks	pale grey-brown

imperialis	Clères hybrid H1	29 and 36 days	not recorded	dark brown	yellow-buff	strong blackish postocular stripe	finely vermiculated brown with strong buff shaft streak and black subterminal spots	finely vermiculated brown with strong buff shaft streak and black subterminal spots	finely vermiculated brown with small black subterminal spots and buff tips	dark brown with strong buff shaft streaks and tips	not recorded
imperialis	Clères hybrid H2	31 days	not recorded	pale tawny	yellow-buff	strong blackish postocular stripe	not recorded	not recorded	finely vermiculated brown with small black subterminal spots and buff tips	rufous-and-black-barred with strong buff shaft streaks and tips	not recorded
imperialis	Clères hybrid H3	35 days	strong black forehead streak	dark brown	yellow-buff	strong blackish postocular stripe	not recorded	not recorded	finely vermiculated brown with small black subterminal spots and buff tips	dark brown with strong buff shaft streaks and tips	not recorded
imperialis	Clères hybrid H4	35 days	not recorded	dark brown	yellow-buff	strong blackish postocular stripe	not recorded	not recorded	finely vermiculated brown with small black subterminal spots and buff tips	finely barred brown and black with strong buff shaft streaks and tips	not recorded
nycthemera berliozi	Clères	33 days	not downy in individual photo-graphed	not downy in individual photo-graphed	rufous-buff	strong blackish postocular stripe	finely dark-barred pale brown with strong pale shaft streaks	finely dark-barred pale brown with strong pale shaft streaks	finely dark-barred pale brown with broad yellow buff tips	finely barred, black, white and buff	pale grey

Table N. Downy chicks

Species	Specimen bird no	Origin	Character				
			Crown pattern	Crown colour	Supercilium	Eye-stripe	Breast colour
edwardsi	*hatinhensis* evidently very similar		strong black forehead streak	tawny brown	whitish to buffy	strong blackish postocular stripe	strongly rufescent
imperialis	AMNH 748400	'one day old'	weak dark forehead streak	pale rufous	very pale rufous	narrow dark brown postocular	washed rufescent
imperialis	BMNH 1930.5.8.1	'hatched 14th May & died 16th May 1930'	strong black forehead stripe	dark brown	whitish	strong blackish postocular stripe	tawny
imperialis	BMNH 1939.6.2.1	'5 days old'	weak dark forehead streak	pale rufescent	whitish	narrow dark brown postocular	pale tawny
imperialis	H1	Clères hybrid, 5 days	not recorded	rufous	rufous-buff	strong blackish postocular stripe	washed rufescent
nycthemera			unpatterned	rufous	rufous-buff	weak, rufescent postocular	little to no rufescent wash

