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**MONOGRAPH**

# A quantitative morphological geographical study from a widely distributed raptor: the Lesser Kestrel *Falco naumanni* Fleischer, 1818 (Falconiformes Falconidae)

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**ABSTRACT** Lesser Kestrel *Falco naumanni* Fleischer, 1818 (Falconiformes Falconidae) is considered a monotypic species. *F. naumanni pekinensis* Swinhoe, 1870 was described from Beijing, China. Although considered valid for most of the 20th century, some authors treated *F. naumanni pekinensis* as a synonym of *F. naumanni naumanni*, and subsequent authors have since regarded "*pekinensis*" as an invalid taxon. Recent field observations in Asia and Europe and museum studies have confirmed diagnosable differences in (fresh) adult males. Comparing morphology between nominate "*naumanni* " and "*pekinensis*", with the latter invariably showing more extensive grey on the wing coverts and darker and more saturated colours on both the underparts and upperparts, with all grey areas, including the hood, being a darker, deeper lead-grey. Females often have more extensive dark markings and a better-defined dark eye-line but apparently are indistinguishable in most cases. This study aims to re-evaluate *F. naumanni pekinensis* and to discuss geographic variation in the subspecies in a widely distributed raptor.

**KEY WORDS** Lesser Kestrel; *pekinensis*; *naumanni*; subspecies; geographical variation.

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## INTRODUCTION

Today, Lesser Kestrel *Falco naumanni* Fleischer, 1818 (Falconiformes Falconidae) is considered a monotypic species (cf. Cramp & Simmons, 1980; Snow & Perrins, 1998; Forsman, 1999; Clark, 1999; Corso, 2000, 2001a; Ferguson-Lees & Christie, 2001). After a few years, was described *F. chenchris pekinensis* Swinhoe, 1870 from two birds (adult male and immature male) (cf. Swinhoe, 1870; Dresser, 1871-1881). Currently, *F. naumanni pekinensis* is regarded as a synonym of *F. naumanni naumanni* (cf. Vaurie, 1965; Dickinson & van Remsen, 2013).

In September-October 2003, two authors (AC, JJ) were at Chokpak Ornithological Station, Jambyl Province, Kazakhstan together with Wim Nap and Arend Wassink, studying raptors and other birds in collaboration with Andrei and Edward Gavrilov as Vladimir Kolbinsev. AC was intrigued by the upperwing pattern of several adult male Lesser Kestrels that were caught in the large Heligoland-traps onsite (and subsequently ringed) as in birds observed in the field. They appeared consistently different from birds AC observed within the Western Palaearctic. The past twelve years, in addition to our field studies of Lesser Kestrel, we have studied

skins from museums worldwide and photos from throughout their breeding range. We have found that eastern populations, especially the well-isolated breeding grounds in China, are phenotypically strikingly different from western populations. This suggests that *F. naumanni pekinensis* may be a well identifiable taxon, although it's breeding and wintering distribution remains to be fully elucidated. This paper reports the preliminary results of our studies concerning western and eastern populations, with a focus on the latter, particularly "*pekinensis*". In this paper we describe plumage colour and pattern, in special fresh adult males, of both Western (*F. naumanni naumanni*) and Eastern Lesser Kestrel (Chinese Lesser Kestrel *F. naumanni pekinensis* and intermediate populations). Their field identification and plumage variability will be discussed separately (Corso et al., personal data).

## MATERIAL AND METHODS

In this study we investigated in detail adult birds in the field within the borders of the Western Palaearctic, and to a more limited extent in Asia. Between 2003 and 2014, we studied birds from Africa (Egypt, Eritrea, Kenya, Morocco, Somalia, Sudan, Tanzania and Tunisia), Asia (Armenia, Azerbaijan, Burma, China, Georgia, India, Israel, Kazakhstan, Laos, Mongolia, Russia, Oman, Turkey, Turkmenistan, Saudi Arabia and Yemen) and Europe (France, Greece, Portugal, Spain and Italy) in field, museum or photographs. During fall 2003, AC and JJ studied tens of Lesser Kestrels in the hand during ringing operations in Kazakhstan as in the field (up to 1.000 birds were observed during their stay). Particular attention was given to the adult males and to a lesser extent to adult females. Juveniles were not studied in much detail.

The skins we studied are held in the following museums and bird collections: American Museum of Natural History, New York, U.S.A. (AMNH); Institute of Zoology, Almaty, Kazakhstan (IZA); Museo Civico di Scienze Naturali "Angelo Priolo", Randazzo, Italy (MCR); Museo Civico di Storia Naturale of Milan, Italy (MCSM); Museo Civico of Terrasini, Italy (MCT); Museo Civico dell'Università di Scienze Naturali of Catania, Italy (MCUCT); Museo Civico di Zoologia of Rome, Italy (MCZR); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museo Regionale di Scienze Naturali of Turin, Italy (MRSN); Museo di Storia Naturale "Giacomo Doria", Genoa, Italy (MSNGD); Museo di Storia Naturale "La Specola", Florence, Italy (MSNLS); National Zoological Museum of China, Beijing, China (NZMC); Naturalis Biodiversity Center, Leiden, the Netherlands (NBC); Natural History Museum, Tring, England (NHM); Naturhistorisches Museum Wien, Vienna, Austria (NMW); Peabody Yale Museum of Natural History, New Haven, U.S.A. (PMNH); Museo Civico di Storia Naturale di Carmagnola, Italy (SNCa); Museum für Naturkunde, Berlin, Germany (ZMB) and in thirteen private collections.

Other abbreviations: AC: Andrea Corso; JJ: Justin J.F.J. Jansen; MV: Michele Viganò.

The list of the specimens (both skins and mounted) examined from the museums and private collections were, after objective examination, divided into four groups (Figs. 1, 2):

Group A: *Falco naumanni pekinensis*: one of two syntypes of the subspecies (Figs. 8, 9); 20 adult males and 8 adult females (China). For Figs. 3, 4, 5 and 6 we used only fresh breeding plumage males from China (N=13).

Group B: *Falco naumanni* ssp.: 28 adult males, 25 females (age combined) (Asia: Mongolia, Altai Mountains breeding area as well as Burma, India and Laos wintering area). For Figs. 3, 4, 5 and 6 we used only fresh breeding plumages males from Mongolia (N=13).

Group C: *Falco naumanni* ssp.: 87 adult males; 60 (age combined) females (Asia: Arabian Peninsula (unspecified countries), Afghanistan, Azerbaijan, Iraq, Kazakhstan, Pakistan, Turkmenistan; Africa: Eritrea, Kenya, Somalia, Tanzania). For Figs. 3, 4, 5 and 6 we used only fresh breeding plumage males from Kazakhstan (N=9), Turkmenistan (N=6), Azerbaijan (N=7) and Afghanistan (N=4).

Group D: *Falco naumanni naumanni*: 349 adult males; 172 (age combined) females (Europe: Albania, Czech Republic, France, Greece, Italy, Macedonia, Portugal, Slovenia, Spain; Africa: Algeria, Angola, Botswana, Egypt, Ethiopia, Libya, Mauritania, Morocco, Niger, Senegal, South Africa, Tanzania, Tunisia; Asia: Armenia, Georgia, Iran, Iraq, Israel, Jordan, Kyrgyzstan, Lebanon, Palestine, Syria, Turkey). For Figs. 3, 4, 5 and 6 we used only fresh breeding plumage males from Turkey (N=5), Greece (N=12), Albania (N=5), France (N=5) and Spain (N=29).

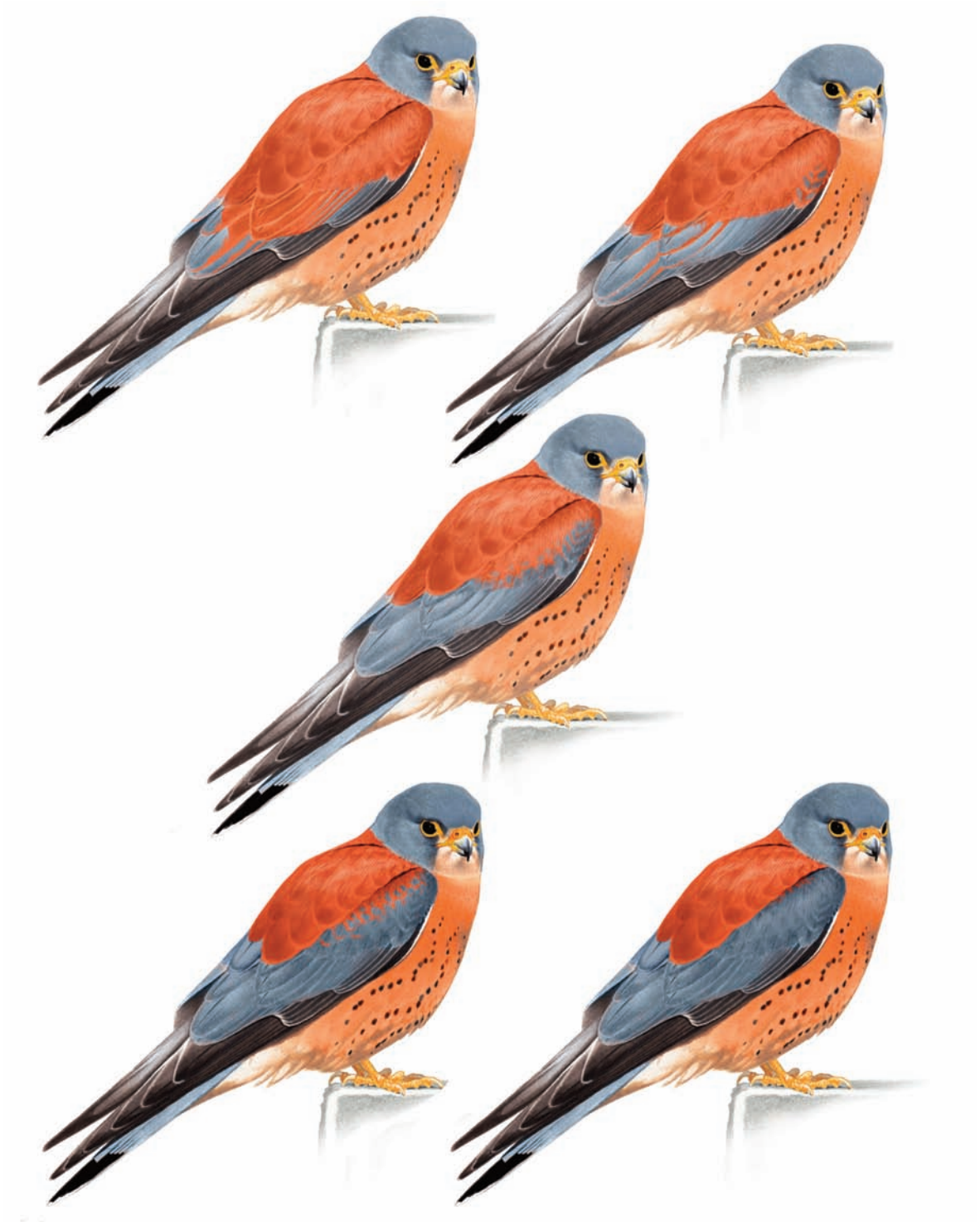

Figure 1. Plumage types as indicated in the text: upper 2 birds (group D), ssp. *naumanni*, among this group, left bird is an example with least grey extension on upperwing coverts and tertials, and on the right typical nominate *naumanni*. Note the grey extension on wing, plumage colour saturation and bare parts colour. Central bird, intermediate bird, plumage group B and C in the text. Lower 2 birds, classic "*pekinensis*", plumage group A, from China breeding populations and allegedly from India, Laos and Burma during winter and on passage. The slight variation found is shown (artwork by Lorenzo Starnini). Note on *pekinensis* that the plumage colour, chiefly mantle and grey tones, is darker, more saturated than nominate *naumanni*, and that the upperwing coverts are entirely grey as well as the bare parts are more orange-ochre.

Additionally, to test the reliability of plumage colour and pattern in discriminating between populations, we took four photographs of each Lesser Kestrel skin. We sampled: upperside, underside and lateral sides (in order to check if there were differences between upperwing pattern of both wings) (Figs. 10-19). We only used indirect sunlight. All specimens were photographed with the same camera at a fixed distance, with a Kodak Gray Scale (Kodak, 2007) in the background (a standard scale of grey values ranging from 0, white to 19, jet black) (Fig. 7). This is an objective way of measuring the grey colours in bird plumages (cf. Adriaens et al., 2010; Bot & Jansen, 2013). The grey card in the background enabled us to calibrate the colours in the photograph, using Adobe Photoshop 10.0.1. We used brightness as a measure to assess the grey and red parts in adult males. To quantify the brightness of the red parts we measured its median spectral reflectance of red, green and blue (RGB) by using Photoshop. To assess the amount of grey and red on the head and upperparts, we measured the saturation. This was calculated by using the formula: saturation = 100 × ((MAX–MIN) / MAX), where MAX and MIN are the maximum and minimum of the median RGB values as measured by Photoshop. A low saturation value corresponds to much grey in the head and upperparts and vice versa. Forthe analysis of colours we used the plates in Ridgway (1912: plate II and III). In particular, we compared the following:

1. Grey value of rump and tail;
2. Grey value of head (hood);
3. Percentage of grey coloured upperwing coverts.

To sample the upperwing coverts, we measured the percentage of grey coloured coverts (versus russet-brown coverts), therefore, how many coverts (median MC+ greater GC+ lesser LC) were grey. On skins, we considered the coverts visible on closed wing by using Photoshop to calculate the percentages. All statistical analysis was performed using R version 2.15.1 (R Development Core Team 2013). Numerical variables (Grey hood and % of grey UPW covers) were tested for normality using the Shapiro-Wilk test. Tests were significant which indicates that these variables do not come from a normally distributed population. Therefore we used a non-parametric approach (Kruskall-Wallis test) to test for a significant difference between groups for these 2 variables. To test for differences between groups in the other 2 variables (colour_of_upperparts and deep_intensity_of_underparts) we used generalized linear models (GLM).

Regarding the specimens and photos of adult females under investigation, we focused on the boldness, width and distribution/demarcation of the dark markings on the head, underwing, tail, mantle and breast. We arbitrary divided specimens on the basis of the extent and boldness of these marking without looking at the label (no geographical preindication), and subsequently checked if these features were related to the classified groups (Fig. 2). After that, we assigned a numerical code to the presence, definition and boldness of the dark markings on the face:

1. no dark eye-line and weak moustache mark;
2. weak eye-line and bolder moustache;
3. obvious and bold dark eye-line as well as moustache.

**The *Falco naumanni pekinensis* syntypes**

Swinhoe (1870: 442) described "*pekinensis*" using an adult male collected on September18th 1868 at the hills overlooking the Ming Tombs (40° 25' 05" N, 116° 22' 41" E) (42 kilometres north-northwest of Beijing) (Figs. 8, 9) and an juvenile male collected at the Western Hills (roughly in Miyun County about 93 kilometres northeast of Beijing (indicative 40°31'40.8"N, 116°48'02.5"E) between 10-12 August 1868 (Swinhoe, 1870: 436).

Specimens from Swinhoe became spread, and the syntype now present in NHM, arrived as part of a load of 480 Accipitres and Striges in three loads in 1886 (Sharpe 1906) donated by Henry Seebohm. Amongst these specimens is the adult male, now labelled as BMNH.1886.3.25.272, and regarded as syntype (Warren 1966: 222). This specimen has been collected according to Warren (1966) and it is labelled as collected on October 18th (sic!) 1868. Henry E. Dresser noted that both specimens in his '*A history of the birds of Europe*'(1871-82, VI: 135) were still in Swinhoe's private collection, and collected in August and September 1868 near Beijing.

A request at electronic Bulletin for European Avian Curators (EBEAC - September 2014) and requests elsewhere did not help in locating the immature male. By chance, a juvenile and adult Amur Falcon *Falco amurensis* Radde, 1863 were collected near Beijing by Swinhoe in August 1868 (Tri-

stram Collection Liverpool T2824 (Tristram, 1889: 67) was reported (Clem Fisher in litteris). Their plumage is notably different, but strangely enough not reported by Swinhoe (1870).

Description: Swinhoe described the types rather briefly: "*Large numbers of Kestrels were flying and hovering about. Their movement struck me as peculiar; and on shooting a male we found the species to be a race of* Falco cenchris, *Naumann. We procured on this occasion an adult male, and in the Western Hills a young male. They agree in size and form with* Falco cenchris *of Europe; but the adult male has all the wing-coverts grey right up to the scapulars, most of them narrowly edged with rufous. The adult has the inner or short primaries broadly bordered at their tips with whitish, rufous in the immature, and wanting in the European bird. Both adult and immature have the white on the under quills 3 ¼ inches short of their tips; in the European bird it advances one inch nearer the tips. I will note this Eastern race as var.* pekinensis. *It will probably be the bird that winters in India.*"

## RESULTS

We sampled 108 fresh adult males from the breeding ranges for this analysis. We sampled the percentage of grey upperwing coverts, grey value in the hood as for the colouration of the colour of

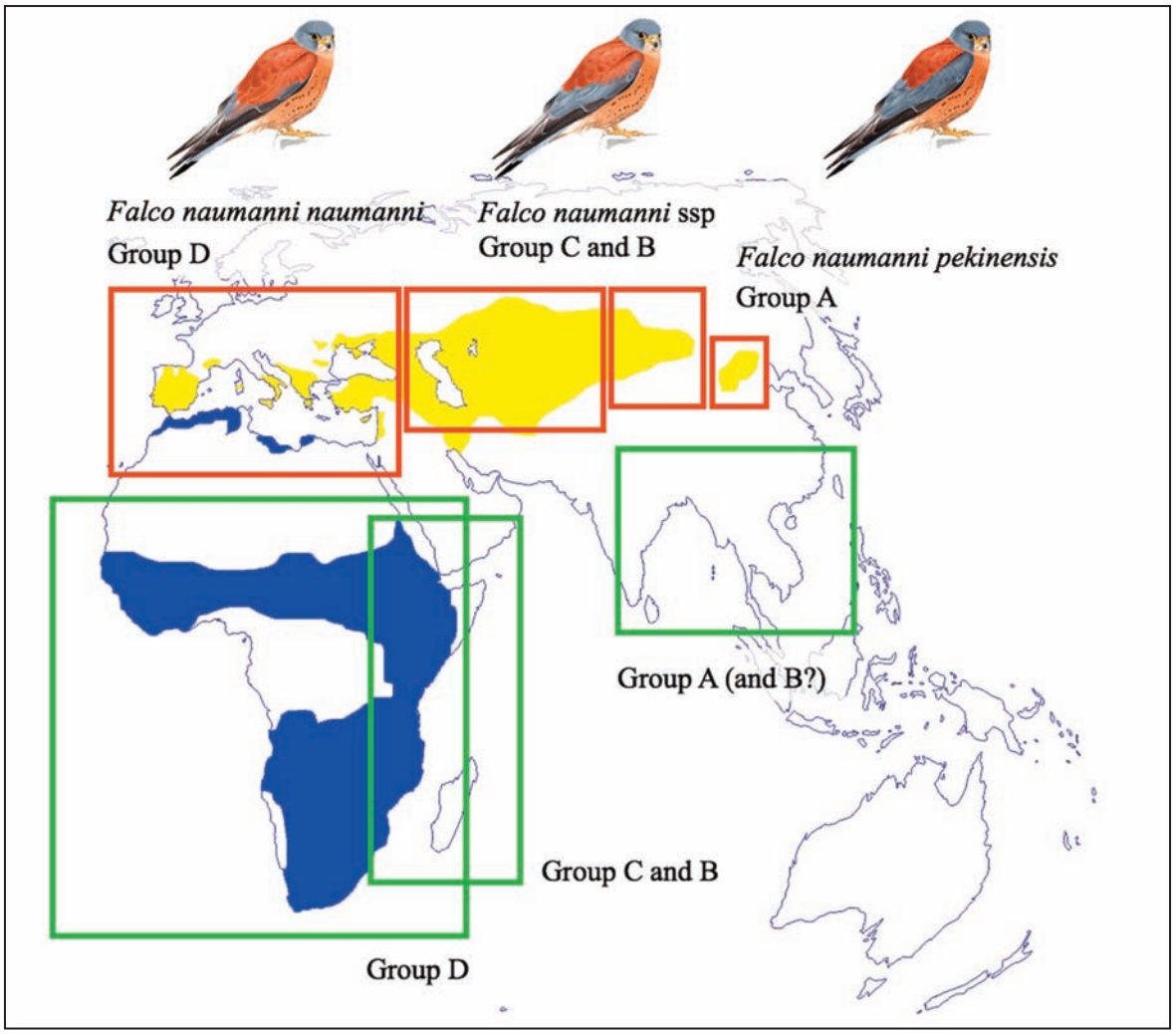


Figure 2. World distribution (breeding range - red, wintering area - green) of the two subspecies discussed in this paper (plumage group A and D), and of intermediate populations and pekinensis-type birds (B/C) as found during this study and according to past literature. Delimitation of the range is roughly indicated and should be considered as solely indicative.

the upperparts and intensity of underparts. The proportion of Group A is 12 %, group B 12 %, group C 24 % and for group D 52 %. Although the proportion of group D is well out of proportion we think the number is sufficiently large to allow good comparison as shown in the results. The results of testing four characters among the four defined areas is summarized in Fig. 2 and also outlined below.

Group A. The adult males collected in China (N=13) show a mean of 11.46 (min. 10; max. 12) on the Kodak Grey Scale (Kodak, 2007) in hood colouration (Figs. 3.7). For grey in the upperwing coverts the mean is 93.5 % (min. 85; max. 99) of grey (Figs. 4, 8, 10, 11, 13, 15, 16). The intensity of underparts is 100 % Mikado-orange mars yellow (Fig. 5). The colouration in upperparts varies slightly as show in Fig. 6, but the mean colouration was Burnt Sienna (8 out of 13 birds). Breeding adult females: 62.5% of the specimens from China (N=8) showed a well-defined dark eye-line (code 3). The remaining (N=3) showed a weaker marking (code 2). However, juveniles of both "*pekinensis*" and "*naumanni*" show a bolder and better-marked moustache and eye-line, compared to adult female, making any relevant use in the field to identify "*pekinensis*" from "*naumanni*" of these characters extremely hard. Concerning the underwing pattern, the outer primaries (wing-tip) as well as the trailing edge of the wing (inner primaries and secondaries) are more extensively and conspicuously dark in all Chinese females than in adult female "*naumanni*" in group D. Also, although rather variable, on average the black bar-like marks on the mantle were wider and more conspicuous than in typical adult female "*naumanni*". Birds from photographs shown a higher amount of variability, with several individuals lacking dark eye-line thus being almost identical to European females but a little darker and more patterned. As for adult male, also in adult female, the cere and the bare skin of the eye-ring, is brighter, deeper coloured and more orange-ochreous than in adult female "*naumanni*".

Group B. The adult males collected in Mongolia (N=13) shows a mean of 8.8 (min. 7; max. 10)on the Kodak Grey Scale (Kodak, 2007) in hood colouration (Fig. 3, 7). For the wing coverts the mean is 71.9 % (min. 50 %; max. 90 %) of grey (Fig. 4) (Kodak, 2007). The intensity of underparts is mixed, as 7 birds are mikado-orange-mars-yellow and 6 are orange-buff (Fig. 5). The colouration in upperparts is mixed, as seen in Fig. 6.

Group C. The adult males collected in Kazakhstan, Turkmenistan, Azerbaijan and Afghanistan (N=26) show a mean of 8.07 (min. 7; max. 10) on the Kodak Grey Scale in hood colouration (Fig. 3, 9) (Kodak, 2007). For the wing coverts the mean is 56.5 % (min. 40 %; max. 86 %) of grey (Fig. 4). The intensity of underparts is mainly orange-buff (20 out of 26) (Fig. 5). The colouration in upperparts varies as shown in Fig. 6.

Group D. The adult males collected Turkey, Greece, Albania, France and Spain (N=56) show a mean of 7.14 (min. 6; max. 10) on the Kodak Grey Scale in hood colouration (Figs. 3, 7) (Kodak, 2007). For the wing coverts the mean is 30.2 % (min. 15; max. 45) of grey (Figs. 1, 4, 17). Notable is the differentiation in western and eastern birds of the distribution are of this population. As we found a certain variability on the extension of the grey coloured upperwing coverts. Some as typical birds as shown in every field guide and handbooks as well as birds showing almost no grey on coverts or only some tinged grey (Figs. 1, 17) in the western part of the distribution area. The intensity of underparts is mostly buff-yellow or capucine-yellow (46 out of 56) (Fig. 5). The colouration in upperparts varies as shown in Fig. 6.

For what concern the female, only 5% of adult females showed a dark eye-line (code 3) (higher percentage when looking at juvenile; Corso, 2000, 2001a; AC pers. obs.). Dark markings on the mantle were on average narrower and less striking than in the most marked adult female *pekinensis*. However, we failed to find relevant differences. In juvenile *naumanni* we found them being darker and with bolder/wider dark markings than adult females, adding to the difficulty to the separate them. Bare parts were less orange and paler, andalways yellower than "*pekinensis*".

## DISCUSSION

The four groups (adult males in fresh plumage) were significantly different when considering the features: hood and % of grey UPW covers (Kruskall-Wallis test) (Table 1). This can be seen in Figs. 3, 4. These figures report averages and standard errors (SE) for each group. The four groups were also significantly different when considering the other two variables (Table 2). Figures 5 and 6 represent

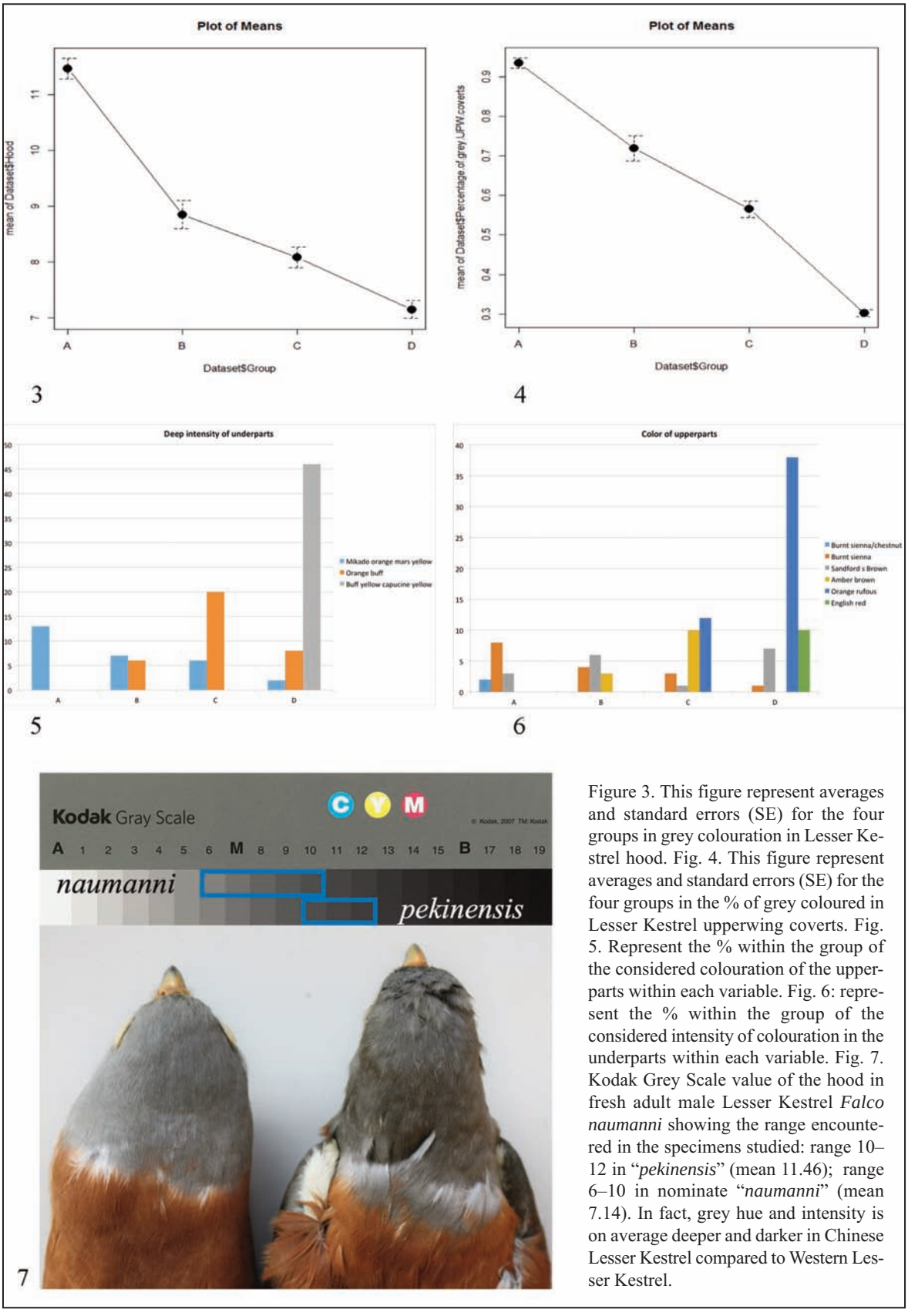


Figure 3. This figure represent averages and standard errors (SE) for the four groups in grey colouration in Lesser Kestrel hood. Fig. 4. This figure represent averages and standard errors (SE) for the four groups in the % of grey coloured in Lesser Kestrel upperwing coverts. Fig. 5. Represent the % within the group of the considered colouration of the upperparts within each variable. Fig. 6: represent the % within the group of the considered intensity of colouration in the underparts within each variable. Fig. 7. Kodak Grey Scale value of the hood in fresh adult male Lesser Kestrel *Falco naumanni* showing the range encountered in the specimens studied: range 10–12 in "*pekinensis*" (mean 11.46); range 6–10 in nominate "*naumanni*" (mean 7.14). In fact, grey hue and intensity is on average deeper and darker in Chinese Lesser Kestrel compared to Western Lesser Kestrel.


Figure 8. *Falco naumanni pekinensis*, adult male Reg. no. BMNH.1886.3.25.272. Near Ming Tombs, north of Peking, 18.X.1868, syntype, R. Swinhoe leg. (H. van Grouw, NHM, Tring). No illustration in any modern field guide is available of such a plumage, with no description or illustration reporting these characters. Fig. 9. *F. naumanni pekinensis*, same bird as plate 5 (H.van Grouw, NHM, Tring). Note the very richly coloured underparts, much richer than any nominate "*naumanni*". Fig. 10. *F. naumanni pekinensis*, adult male, Hebei, China, 27.IV.1937 (He Peng, NZMC). A fresh adult male "*pekinensis*" from the typical breeding range of the taxon, showing very intense brick-red (Burnt Sienna) mantle and sooty-led grey plumage areas. Fig. 11. *F. naumanni pekinensis*, adult male, Hebei, China, 27.IV.1937 (He Peng, NZMC). Same bird of Figs. 10, 12. Note that the entire upperwing coverts are typically solidly dark sooty led-grey, as never shown by any nominate "*naumanni*". Fig. 12. *F. naumanni pekinensis*, adult male from Hebei, China, 27.IV.1937 (He Peng, NZMC). Same bird of Figs.10, 11 Note the very richly coloured underparts, more saturated and extensively coloured than in typical nominate "*naumanni*".

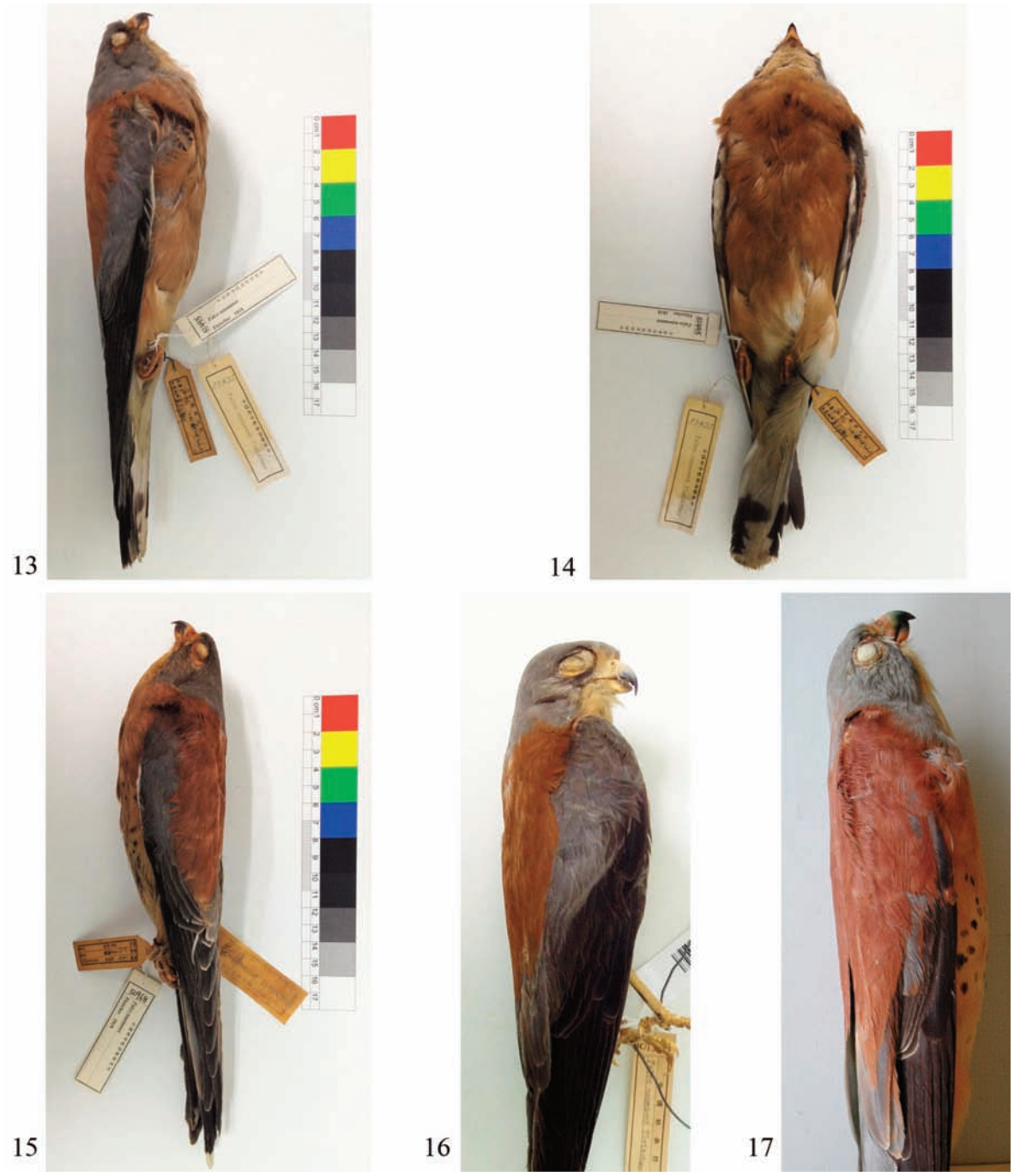


Figure 13. *Falco naumanni pekinensis*, adult male, Bejing, China, 4.IV.1961 (He Peng, NZMC). Note the typically entirely grey upperwing coverts of this male from the terra typica of the *pekinensis* taxon. Fig. 14. *F. naumanni pekinensis,* adult male, Bejing, China, 4.IV.1961 (He Peng, NZMC). Same bird of Fig. 15. Note intensely coloured underparts, with very saturated colour. Fig. 15. *Falco naumanni pekinensis*, adult male, Hebei, China, 8.X.1965 (He Peng, NZMC). Note that the entire upperwing coverts are typically solidly dark sooty led-grey, as never shown by any nominate *naumanni*. Fig. 16. *F. naumanni pekinensis*, adult male, Hebei, China, 27.IV.1937 (He Peng, NZMC). Same bird of Figs. 10,12 to show a close up view of the upperwing coverts pattern. Compare to Fig. 17. Fig. 17. *F. naumanni pekinensis*, ad. male, Spain (A. Corso, NHM, Tring). Plumage type D according to description given in the text. Note that in many European birds (ca.20%) the grey on wing coverts is very limited and pretty hard to be seen in the field or even in the hands. Note that the plumage is paler, less intense and less deep in both the grey of hood and wing-coverts and of the mantle and underparts.

the percentage within group of the considered category within each variable. The analyses showed that the groups are significantly different. The largest difference was found between group A and D (Tables 1, 2).

These groups, possibly, connect in winter/migration areas, but more study is necessary. Also the wintering areas for the individual groups are unknown, but in Fig. 2 we displayed the supposed wintering areas. The differences between group A and D is large and both phenotypes differ 86.2% taken into account the four sampled morphological features. We did not investigate whether there are genetic differences among "*naumanni*" and "*pekinensis*", something that surely should be the target of future studies. The mean differences between other groups are A vs. B 49 %, A vs. C 75 %, B vs. C 14.7%, B vs. D 67.8% and C vs. D 39.3 %.

According to the criteria to show discrete character differences (Rolán-Alvarez & Rolán, 1995; Corbet, 1997; Johnson et al., 1999; Garnett & Christidis, 2007; Rising, 2007; Winker et al., 2007; Cicero, 2010; Remsen, 2010) 86.2 % fall well in the criteria set by Amadon (1949), Simpson & Roe (1939) and Mayr (1969) (George Sangster in litteris). We advise that the Chinese population known under the synonym "*pekinensis*" should be considered valid, despite the apparent intermediate zone between this and nominate "*naumanni*". For the Lesser Kestrel the same applies as for other polytypic species of raptor with a wide breeding distribution area that it has a certain amount of clinal variation (Ferguson-Lees & Christie, 2001). Examples are Common Buzzard *Buteo buteo* ssp., Black Kite *Milvus migrans* ssp., Saker Falco cherrug and Peregrine *Falco peregrinus* ssp. (Vaurie, 1961; Ellis & Garat, 1983; Brosset, 1986; Dixon et al., 2012; White et al., 2013). The distributional areas are often poorly defined and a large variability applies in subspecies (Dementiev, 1957; Corso, 2001b; Eastham et al., 2001; Brichetti & Fracasso, 2003; Eastham & Nicholls, 2005; Karyakin & Pfeffer, 2009; Pfeffer, 2009; Zuberogoitia et al., 2009; Karyakin, 2011; Rodrìguez et al., 2011). To meet the criteria as set by Amadon (1949), Simpson & Roe (1939) and Mayr (1969) most currently recognised subspecies fall short when assessed on the overlap between phenotypes.

To simplify, we are faced with two choices: 1) we consider the currently recognized subspecies of a forementioned raptor species and other wide-ranging raptors as representatives of clinal variation only. And therefore unworthy of taxonomic rank, in which case we would not consider "*pekinensis*" as a valid taxon in light of the intermediate birds found; 2) we believe all these taxa, including "*pekinensis*", to be worthy of taxonomic rank. In any case, as the Chinese population of Lesser Kestrel is always identifiable, and geographically isolated. It is therefore worthy of taxonomic rank, which will also help focus attention on its conservation (Patten, 2015).

| Variable | Chi squared | df | Pr(>Chi |
|---|---|---|---|
| Kodak_hood | 53,62 | 3 | <0.01*** |
| percentage_of_grey_UPW_coverts | 89,2 | 3 | <0.01*** |

Table 1. Showing the Kruskall-Wallis test at all four groups, considering hood and % of grey upperwing coverts.

| Variable | Chi squared | df | Pr(>Chi |
|---|---|---|---|
| colour_of_upperparts | 30,73 | 3 | <0.01*** |
| deep_intensity_of_underparts | 94,79 | 3 | <0.01*** |

Table 2. Showing GLM test, on the colouration of upperparts and the intensity of underparts.

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