

The Gyrfalcon

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The Gyrfalcon.—Eugene Potapov and Richard Sale. 2005. Yale University Press, New Haven, Connecticut. 288 pp. ISBN 0-300-10778-1. Cloth, \$45.—Latest in what has been a distinguished Poyser series of monographs on birds of prey, this book is mainly a descriptive biology of the Gyrfalcon (*Falco rusticolus*)—the largest of falcons, circumpolar in distribution, and with unique adaptations to life in harsh Arctic environments. The first nine chapters treat paleobiography and systematics; identification and colors; distribution; population; habitat and landscape preferences; food and feeding habits; breeding cycle; dispersal, seasonal movements, and winter distribution; and competitors, commensals, and conspecifics. The final two chapters deal with man and falcons and threats and conservation.

Because neither author has done much original research on the Gyrfalcon, their book is mainly a review of the literature, though they present original research on morphometrics and plumage variations based on extensive examination of museum skins. By far the most important contribution of this book is its comprehensive summary of the Russian literature on the Gyrfalcon, much of which

occurs in rather obscure sources. Being Russian, with a developing ability to communicate in English, Potapov is qualified to bridge the two languages, but he needed more help than he evidently got from his editors and coauthor in smoothing out rough passages of text. Even so, it is exciting to read details about the natural history of the Gyrfalcon from the first-hand accounts of Russian field workers searching out the vast expanses of the Russian and Siberian northlands for this rare falcon. The ~500 references include no fewer than 162 Russian titles (translated). Finnish and Scandinavian languages are also well represented and, overall, the list of titles is a rich compendium of the world literature on the Gyrfalcon.

Unfortunately, the book was not well edited and contains many errors—omission of words, tandem duplication of the same word, misspellings (including authors' names and scientific names), and confusions resulting from poor use of English. The legends for some figures and plates lack sufficient information to allow the reader to interpret what the depicted data are supposed to represent (see especially figs. 2.1, 2.2, and 2.3 and plates 3–7 dealing with plumage color and pattern). In all, I found more than 260 errors and confusions in 280 pages of text and references. Clearly, the manuscript for this book needed meticulous copyediting, which it did not receive.

Chapter 1, with Olga Potapova as senior author, presents an interesting paleogeographic theory to explain how the proto-Gyrfalcon population became geographically isolated from the ancestral Saker (*F. cherrug*) or Saker-Gyrfalcon common ancestor as a result of an uninhabitable barrier of larch forest that spread across Eurasia, separating the northern tundra grasslands from the southern steppes, starting around 9,000 BP. One problem with this explanation is whether or not the genetic and phenotypic differentiations between Gyrfalcons and Sakers could have taken place in less than 10,000 years BP. Wink et al. (2004) estimated—from interspecific genetic distances ranging from 0.4% to 2.0% among falcon species in the *Hierofalco* group, which includes the Saker and Gyrfalcon—that this amount of differentiation would have occurred in a period of 200,000–1,000,000 years BP. They further pointed out that among other bird families, such small genetic distances indicate taxonomic differentiation at no more

than the level of subspecies. In that regard, as Potapova et al. point out, the Gyrfalcon and Saker breeding populations remain totally allopatric, unless the much-discussed "Altai Falcon" in the mountains of central Asia represents a hybridized population of the two forms. Also, in captivity the two forms are fully fertile at least through the F_3 to F_4 generations, which indicates an absence of reproductive isolating mechanisms. The accumulating data point to the likelihood that the Gyrfalcon and Saker are allopatric populations of the same species (Cade et al. 1998); even so, it is difficult to understand how the differences between them could have accumulated in less than 10,000 years. Work on other groups of avian species involving estimates of species divergence times based on molecular systematics and "clocks" indicate that most recent species divergence events occurred from 1 to 5 million years ago and that late Pleistocene isolations caused by glaciation and associated climate-induced changes in biomes occurred too recently to account for speciation events (Klicka and Zink 1997).

Ever since publication of the 10th edition of *Systema Naturae* (Linnaeus 1758), argument has raged over the correct binomial for the Gyrfalcon (Hartert 1915, Lönnberg 1931, Dementiev 1960, Banks and Browning 1995). At least since the 11th century, the Gyrfalcon was known in Latin treatises on natural history and falconry as *gyrofalco* or *gyrofalco* (and other variations), and in his 10th edition, Linnaeus (1758) described a bird of prey under the name *Falco gyrfalco*. His verbal description is marginally adequate to fit the Gyrfalcon, but he also referred to a picture of a Northern Goshawk (*Accipiter gentilis*) published under the name *F. gyrfalco* in his earlier work, *Fauna Svecica* (1746), thereby invalidating the use of this name for the Gyrfalcon, according to Lönnberg (1931). A name having page priority (first use) in the 10th edition (Linnaeus 1758) is *F. rusticolus*, but the diagnosis accompanying this name is less clearly referable to the Gyrfalcon than that of *F. gyrfalco* and should be rejected as a *nomen dubium* according to Potapov and Sale. Hartert (1915), the *de facto* "first reviser" of the Gyrfalcon's nomenclature (not Lönnberg [1931], as the authors state), became convinced that *rusticolus* is the correct name, and it is the one that has been in most general use in the post-Linnaean period, except in Russia, where several authorities, notably

Peter Pallas and G. P. Dementiev, continued to use *gyrfalco*. Potapov and Sale lead us through the modernized but still byzantine International Code of Zoological Nomenclature (4th edition, 1999) in an effort to prove that the Russians are right. One hopes their arguments are convincing and that the International Commission will one day validate the historical and most apposite name, *Falco gyrfalco*.

One of the potential strengths of this book is that Potapov personally examined more than 1,800 museum specimens from 10 major collections, certainly the largest series ever studied. These specimens come from all parts of the Gyrfalcon's circumpolar range, though more than 48% come from Greenland and more than 23% from Iceland. Furthermore, only 402 specimens were collected during the nesting season and can be more or less reliably assigned to a breeding range. The mensural data were analyzed to determine sexual differences in size (figs. 1.2–1.5), but geographic differences are treated poorly and often rely on previously published analyses (e.g., Table 1.4). With their large data set, the authors missed an opportunity to re-examine published generalities about geographic trends (e.g., a decrease in size from south to north in Greenland, the reverse of Bergman's rule [Salomonsen 1951]; a trend of size increase from west to east across Eurasia [Dementiev 1960]).

The most difficult part of the book, in chapter 2, deals with colors and color patterns. The plumage of the Gyrfalcon shows such a high degree of individual variation that researchers have long struggled to explain its taxonomic, geographic, and biological significance. In the immediate post-Linnaean period, strikingly different variants were considered separate species: white birds belonged to *F. (Hiero) falco*, gray birds on Iceland were *F. islandus*, and J. J. Audubon named the dark birds of Labrador *F. labradorus*, and so on. As it became evident that all these forms were capable of interbreeding and producing intermediate variants, many of the species names were redesignated as subspecies. In the 1930s through 1950s, Danish researchers, working mainly with Greenlandic Gyrfalcons, developed their popular "trimorphic" explanation based on their recognition of white, gray, and dark (brown) "color phases." Their concept involved a combination of subspecies designations and the recognition of more-or-less distinct color phases, which

others later transformed into “morphs,” forms that are supposed to be disjunctively different from each other (Flann 2003). The whole system from north to south was described as a “trimorphic ratio cline” (Salomonsen 1951).

Cade (1960) and Vaurie (1961) concluded that there are no clear geographic patterns of variation that justify designation of subspecies. Cade et al. (1998) and Flann (2003) further pointed out that too many intermediate variants exist between white and gray, and between gray and dark, to justify use of the concepts “polymorphism” and “morph” to describe this variation, because by definition morphs must be phenotypically and genetically disjunct from each other.

Potapov and Sale open their discussion of plumage variation with a consideration of “the true colour of Gyrfalcons” and provide original data on the reflectance spectra of various plumage regions for white, gray, and dark “morphs,” with emphasis on the possibility of ultraviolet reflectance and its biological significance. They assume that Gyrfalcons have visual capability in the ultraviolet (UV) range as some other birds do, though there is no proof. The reflectance spectra reveal that the “white” parts of feathers reflect only from wavelengths of 450–500 nm in the red, near-green, and green parts of the spectrum and are not really white; there is no UV reflectance from any part of the feathers; and thus, even if they have UV vision, Gyrfalcons cannot be using ultraviolet patterns in their plumage as signals for social behavior.

There follows some rambling discussion about the color of snow, which is highly UV reflective (no data provided), and the color of white prey such as ptarmigan, Arctic hare, and collared lemming. The biological significance of the presence or absence of UV reflectance is not really explained. Apparently, a white prey with no UV reflectance would be visible as a “shadow” against a snowy background by a predator with UV vision, and vice versa.

By categorizing and analyzing the plumage characters of 1,310 specimens of adult Gyrfalcons into 26 color and pattern codes (table 2.1 and plates 3–7), the authors claim to have demonstrated that instead of the classical three color morphs, there are in fact two color morphs (“pure white” and “melanistic”) and two pattern morphs (regularly and irregularly barred feathers). Nothing is said about where the gray birds fit into this overall scheme of

variation. Data from the plumage codes were subjected in some unexplained way to principal component analysis (PCA; fig. 2.2), and from this analysis the authors conclude that there are (page 57) “consistent color patterns on various parts of the body which form clusters,” which suggests that belief in “the existence of continuous variation in Gyrfalcons is probably incorrect.” They allow, however, that (page 58)

there is probably a continuum of intergradation from white to black (of white to dark background of feathers, or absent to high-intensity pigmentation of the pattern), but it works on the individual axes of the three-dimensional plots of patterns that we have generated, and thus results in the discrete patterns we see in Gyrfalcons.

The entire explanation of color patterns (pages 54–58) is extremely confused, and not enough information is provided about how the authors carried out their PCA to allow readers to form their own judgment of what the data in figure 2.2 mean. Moreover, in plates 3–7, which depict representative examples of “plumage codes” for various parts of the body, the percentages for subtypes of the various codes do not add up to the total percentage of the code under which they are subsumed, often by a substantial difference. It is unclear whether these differences result from miscalculations or from something not apparent in the way these percentages are presented.

Instead of shedding light on the complicated plumage variation of the Gyrfalcon, these authors have added to the existing confusion created by the continued use of the term “morph” to categorize plumage variants of this species (Flann 2003). In their glossary, the authors define “colour morph” without reference to discontinuity between the variants. Visual inspection of the plumage categories shown in plates 3–7 appear to confirm that the variations in color and pattern are continuous.

The chapter on “man and falcons” is based largely on the classic anthropological writings in Shternberg (1925, 1936), and while interesting, much of it is not directly relevant to the Gyrfalcon. The other principal source is G. P. Dementiev’s (1960) fine essay on involvement of the Gyrfalcon in the medieval culture of falconry in czarist Russia and Europe. The depiction of Emperor Frederick II of Hohenstaufen in

Russian garb, holding a modern hood with braces (fig. 10.1), is rather bizarre. The book ends optimistically and calls attention to the value of harsh and remote environments as protective factors for some species, even for one as sought-after as the Gyrfalcon, which still thrives in most parts of its range.

To summarize, this is a rather unfortunate book. Among other faults, the pictures and maps are poorly produced. The work serves as the only adequate review of the world literature on one of the most interesting and charismatic birds; but the inquiring reader is likely to be disappointed by lack of synthesis and summary of the many details presented, and the often difficult text must be read with care.—TOM J. CADE, *The Peregrine Fund*, 5668 Flying Hawk Lane, Boise, Idaho 83709, USA. E-mail: tcade@peregrinefund.org

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