

SHORT COMMUNICATIONS

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PRONOUNCED VARIATION IN TARSAL AND FOOT FEATHERING IN THE UPLAND BUZZARD (*BUTEO HEMILASIUS*) IN MONGOLIA

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During 1994, 1995, 1997 and 1998, we located over 250 Upland Buzzard (*Buteo hemilasius*) nests across Mongolia. In these nests, we noted considerable morphological variation in plumage coloration and in leg pterylosis of nestlings. Although it is normal for many *Buteo* species to display a high degree of color polymorphism, the variability we found in tarsal and foot feathering was unique and sometimes greater within a single brood than could be expected within any naturally occurring raptor species.

Although Brown and Amadon (1968) illustrated the Upland Buzzard as bare-legged, their text states that the tarsus is partially feathered and Weick (1980) illustrated partial tarsal feathering. We found that more than half of the birds in Mongolia have fully feathered tarsi (Fig. 1a) while others, sometimes in the same nest, had tarsi three-quarters or even half feathered (Fig. 1b). Occasionally birds had patches of feathers or scattered feathers on their tarsi (Fig. 1b, c), and, less frequently, feathers on their toes (Fig. 1d).

Because of the variety of leg feathering that we observed during our first two expeditions, in 1997 and 1998 we examined 131 nests scattered across eastern and central Mongolia and report here the tarsal condition of 119 nestlings from 59 broods where young were at least 2 wk of age (i.e., we excluded younger nestlings to minimize confusion over ontogenic changes). Because developmental photos are unavailable for Upland Buzzards which Zhang (1984) claims fledge at 7 wk, we estimated

age by comparison with Moritsch's (1983) photos of Red-tailed Hawks (*B. jamaicensis*) which fledge at about 6 wk of age.

Feather condition was as follows: 69 nestlings had tarsi fully feathered (i.e., feathers extended [or would have extended when fully grown] from the ankle all the way to the base of the toes), 32 were three-quarters feathered and 18 were half feathered. Of the 119 nestlings, 16 had scattered feathers on their tarsi or feet beyond the zone of continuous feathering. Among the 69 nestlings with full tarsal feathering, four had scattered feathers between or on their toes. Another bird with only three-quarters feathered tarsi also had scattered feathers on its toes. Of the 11 nestlings with feathers scattered on their tarsi, eight were among the 18 nestlings with tarsi half feathered. For two nestlings, distribution of feathers was doubly odd. The lateral aspect of both tarsi were half feathered, while the medial sides were nearly fully feathered.

In summary, of 119 nestlings we carefully examined, 50 (42%) had less than fully feathered tarsi and four of the 69 with fully feathered tarsi had scattered feathers on their toes. Thus, 54 of 119 birds (45%) in some way deviated from the feathered tarsi-bare toes condition. Of this 54, 16 (13% of 119) had scattered feathers on either tarsi or toes. Observation of an occasional aberrant specimen in a population is not surprising, but for 13% of the population to exhibit such a conspicuous aberrancy (i.e., scattered feathers in otherwise scaled areas) strongly suggests allelic segregation beyond what would be expected without hybridization. Further, 42% of the young had significantly exposed (i.e., scaled) tarsi, even though



Figure 1a. Recently fledged, dark morph, Upland Buzzard from central Mongolia. This bird shows small pale breast patch suggestive of Long-legged Buzzard dark morph birds but fully feathered tarsus like about half of the Upland Buzzards in our sample. This bird is a brood mate of the fledgling in Fig. 1c. Figure 1b. Tarsi of Upland Buzzard nestlings in eastern Mongolia. Upper, half-feathered tarsus with a disjunct line or patch of feathers. Lower, three-

tarsal feathering has obvious adaptive advantages in cold climates.

The variability that we saw in tarsal feathering in the Upland Buzzard in Mongolia rivals the variability achieved after many generations of selective breeding in domestic varieties of chickens (*Gallus domesticus*) and Rock Doves (*Columba livia*). Poultry breeders have concluded that one or two independent autosomal genes are responsible for shank feathering in several breeds of chickens. The interaction of these genes produces the different patterns and the extent of feathering noted in various breeds (Hutt 1949). Three classes of leg feathering are recognized in pigeons, with the "grouse pattern" more closely resembling the condition observed in feather-legged raptors. The mechanism for inheritance of this trait is not clear, but the gene appears to be autosomal (Levi 1986). It is not uncommon in both poultry and pigeons for clean-legged birds to grow a few short feathers on the tarsi or show pin feathers on the toes. Levi (1986) found that a strain of clean-legged pigeons continued to throw some pin feathers after 35 yr of selection against feathered legs. Apparently more than one autosomal gene is responsible for these scattered feathers and the alleles responsible may be recessive.

The genetics of tarsal feathering in raptors is unknown, nor do we know of any publication indicating that there is any considerable variation for the trait within either feather-legged or bare-tarsi species. The extreme variation observed in Mongolian Upland Buzzards is believed to be unique. It is germane that some authors treat the Upland Buzzard as conspecific with the Long-legged Buzzard (*B. rufinus*, Vaurie 1961), a species with bare tarsi (Brown and Amadon 1968, Weick 1980). It is pertinent that the only bare-legged Upland Buzzard we noted on any of our expeditions was in western Mongolia and within Vaurie's (1961) zone of Upland and Long-legged Buzzard sympatry. Also pertinent to the hybridization question is Vaurie's (1961) map showing that the easternmost extension of the breeding range of the Upland Buzzard is only 600 km west of and at the same latitude as the southern extension of the range of the Rough-legged Buzzard (*B. lagopus*), a species with consistently feathered tarsi. Galushin (1981) mentions a nesting record of the Upland Buzzard on the Amur River that is even further east than the eastern limit mapped by Vaurie. Further, Vaurie shows that Rough-legged Buzzards occasionally breed only about 700 km north of the western range of both Upland and Long-legged Buzzards. There is re-

markable similarity between many light morph Rough-legged and Upland Buzzards. Further, many dark morph Upland and Long-legged Buzzards have a unique light crescent on an otherwise dark breast and both sometimes have a light patch on the crown and forehead (Brown and Amadon 1968, Plate 107; Fig. 1a, c).

The most likely explanation of this tarsal and foot feathering anomaly and these plumage similarities is that extensive hybridization is ongoing between Upland and Long-legged Buzzards. Alternately, the Upland Buzzard may be the result of a major hybridization event between Long-legged and Rough-legged Buzzards in the recent past. If either (or both) of these possibilities is (are) true, we expect that careful morphological comparisons for other anatomical features of Upland Buzzard specimens will also show extreme variability. Another, but we think unlikely, explanation is that the variability that we noted is simply the norm for the Upland Buzzard.

In explaining this anomaly, it may be helpful to examine Rough-legged Buzzard nestlings around the Sea of Okhotsk and Long-legged Buzzard nestlings in northwestern China and eastern Kazakhstan, or other zones of sympatry with the Upland Buzzard. Field teams working outside of Mongolia could provide useful comparative data on other Upland Buzzard populations as well. In 1997, we gathered blood samples for genetic analysis in the expectation that comparison of DNA for the three "species" will ultimately resolve this interesting question.

RESUMEN.—Casi la mitad de 119 pichones de *Buteo hemilasius* observados en Mongolia, mostraron tarsos y garras emplumadas en forma distinta a lo esperado (tarsos emplumados, garras desnudas). Muchos mostraron parches de plumas en áreas desnudas de tarsos y garras. Este extraordinario grado de variabilidad puede ser explicado como el resultado de una extensiva y reciente hibridación entre *Buteo rufinus* y *Buteo lagopus* y/o entre *Buteo rufinus* y *Buteo hemilasius*.

[Traducción de César Márquez]

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fourths feathered tarsus. Figure 1c. Fledgling, dark morph Upland Buzzard (brood mate of the bird in Fig. 1a) with extensive pale patches on breast and head like that known for the dark morph of the Long-legged Buzzard. The tarsus is half feathered with a more distal, disjunct patch of feathers. Figure 1d. Tarsi of nestling Upland Buzzards in eastern Mongolia. Both birds will have fully feathered tarsi (when hard-penned) and both have a scattering of feathers on the toes.

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CLOSE INBREEDING IN PEREGRINE FALCONS IN MIDWESTERN UNITED STATES

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Selection against inbreeding is usually assumed to be an important factor in the evolution of dispersal patterns in animals (Thornhill 1993), because close inbreeding increases the probability of expression of deleterious recessive genes. We have identified several cases of close inbreeding (here defined as mating between siblings, half-siblings or parents and offspring) in Peregrine Falcons (*Falco peregrinus*) in the midwestern United States. This paper discusses the possible causes and consequences of these inbreeding events.

The current midwestern peregrine population originated from 857 captive-bred falcons released since 1982 as a part of the continent-wide effort to reestablish populations of the species in areas where they had been eliminated or reduced by poisoning by DDT and related compounds. Midwest as here used includes Minnesota, Wisconsin, Michigan, Nebraska, Iowa, Illinois, Indiana, Ohio, Kansas, Missouri, Kentucky, southeastern Manitoba and the Lake Superior basin of Ontario. We have already shown for this new population (Tordoff and Redig 1997), numbering 99 territorial pairs in 1998, that: 72% nest on man-made structures and 28% on cliffs. First breeding is usually at age two, although some females and fewer

males begin at one year of age. First-year survival is probably close to 40% and annual survival of adults is 86%. Dispersal from hatch or natal sites has huge variation (range 0->1500 km for both sexes, but mean dispersal of females (323 km) is about twice that of males (176 km).

Peregrines released in the restoration effort have passed through three bottlenecks, each of which must have reduced genetic variation in the population. The first was the pesticide-induced reduction in size of wild populations from which captive birds were drawn. Second, captive-breeding peregrines represented a small sample of the wild populations from which they were taken. The number of true founders (unrelated ancestors brought in from the wild for captive breeding) for the new midwestern population was 70-80 individuals. Third, a founder's contribution of genetic material to the wild population is determined by differential reproduction in captivity, which is probably more pronounced than in the wild.

Only about one-fourth of fledged young, released or wild-produced, actually become breeders in the wild. Through 1996, 1383 peregrines were known to have fledged in the Midwest (757 hatched, 626 wild); through 1998, about 290 (21%) of these were known to have become breeders, although some additional birds fledged