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Brandt's Vole density affects nutritional condition of Upland Buzzard *Buteo hemilasius* on the Mongolian Grassland Steppe

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We evaluated the nutritional condition of nestling Upland Buzzards by using the non-invasive ptilochronology technique. Recognizing that each growth bar on a feather represents 24h of growth, this technique uses the width of growth bars as an index of a bird's nutritional condition at the time the feather was being grown. Despite the fact that ptilochronology has been used in raptors, there is no experimental evidence that growth-bar width reflects dietary adequacy in Upland Buzzards. Field work was conducted during the 2007 breeding season in Central Mongolia, in two separate areas that had different densities of Brandt's Vole, the main prey of the focal species. The average Brandt's vole density of 18 different plots in the Eej Khad study area was 441.6 ind/ha. In the desert steppe, the density was zero during the same period of time. Growth-bar width of nestlings was significantly different and wider in vole-rich areas than in areas lacking voles (3.9 vs. 2.24 mm/24-h period). Similarly, there was a significant difference in the number of fault bars; the average was 2.2 in vole-rich areas and 0.5 in areas with no voles. Prey abundance also influenced the average clutch size that was larger in vole-rich areas (4.1 vs. 2.8), resulting in the fledging of a greater number of young (3.8 vs. 2.4).

1. Introduction

The Upland Buzzard (*Buteo hemilasius*) is a monotypic, but dimorphic and variable species. It is considered to be closely related to the Long-legged Buzzard (*B. rufinus*) with which it forms a superspecies. Its breeding distribution is confined to the eastern Palaearctic (ca. from 53º to 30º N). The majority occur in Mongolia, but its range extends from the south of Siberian Russia in the north to northern and central China in the south (Ferguson-Lees & Christie 2001).

In Mongolia, the Upland Buzzard breeds from the Altai Mountains to the western foothills of the Great Khyangan Mountains (Fomin & Bold 1991). To date, most work on this species relates to its distribution, density, status, diet, and breeding biology in Mongolia (Przewalskii 1876, Pevtsov 1883, Bianki 1915, Tugarinov 1932, Sushkin 1938, Kozlova 1930, 1975, Minoransii 1962, Dementiev 1963, Mauersberger 1980, Piechocki *et al.* 1981, Flint & Bold 1991, Stephan 1994a, b, Bold *et al.* 1996, Sumiya & Batsaikhan 1999, Bold & Boldbaatar 2001, Potapov *et al.* 2001, 2005,

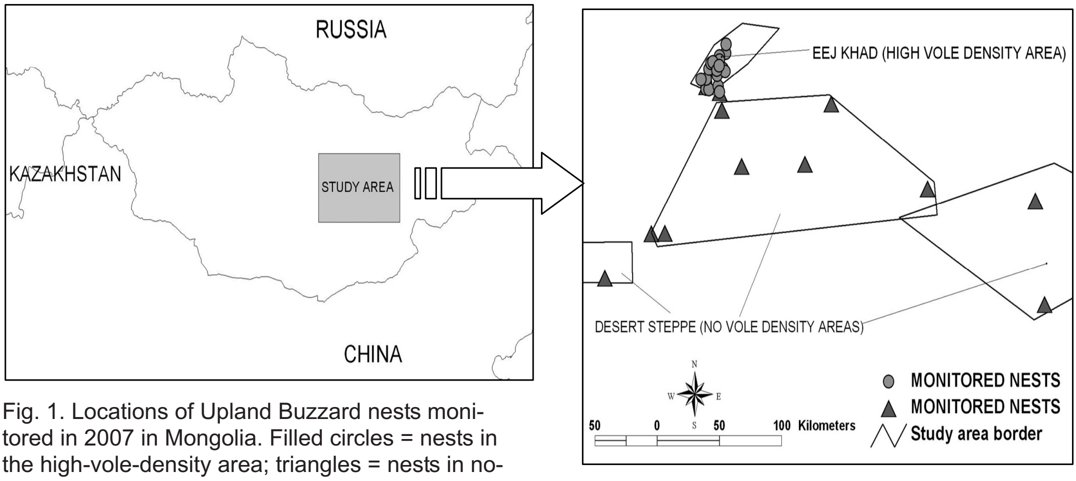

Fig. 1. Locations of Upland Buzzard nests monitored in 2007 in Mongolia. Filled circles = nests in the high-vole-density area; triangles = nests in no-vole areas (desert steppe).

Gombobaatar 2006, Gombobaatar *et al.* 2006, 2008, Mainjargal 2006). There are comparatively few descriptive studies of the breeding biology of the species (Shagdarsuren 1964, 1983, Bold & Boldbaatar 2001, Karyakin 2005, Karyakin & Novikova 2006, Karyakin *et al.* 2005, 2006, Gombobaatar 2006) and to date, there are no detailed descriptions of the relative growth rates of nestlings and their relative nutritional condition. Past studies have reported that the number of breeding pairs of Upland Buzzard, and their breeding success, was highly dependent on the density of the Brandt's Vole (*Lasiopodomys brandtii*; Bold & Boldbaatar 2001, Gombobaatar *et al.* 2005, Potapov *et al.* 2004, Potapov 2005). Thus, we monitored active nests in areas with vole densities of two extremes: very high in the Eej Khad area and none in the Desert Steppe (Choir regional center, indicated by 'sum' below, Gobisumber province Delgertsogt, Gobi-Ugtaal sum, Dundgobi province, Dalanjargalan sum, Dornogobi province; Fig. 1).

Hence, to evaluate the effect of prey density on nestling growth rate and subsequent fledging success, we evaluated the nutritional condition of the nestlings by using the non-invasive ptilochronology technique (cf. Grubb 1989, 1991, Grubb & Yosef 1994, Yosef & Grubb 1992). Recognizing that each growth bar on a feather represents 24h of growth (Brodin 1993), this technique uses the width of growth bars as an index of a bird's nutritional condition at the time the feather was being grown (Grubb & Yosef 1994). Although Murphy and King (1991) did not measure growth-bar width, they found that daily feather growth was reduced in White-crowned Sparrows (*Zonotrichia leucophrys*) maintained on deficient diets. Despite the fact that ptilochronology has been used in raptors, such as Osprey (*Pandion haliaetus*; Machmer *et al.* 1992), American Kestrel (*Falco sparverius*; Bortolotti *et al.* 2002) and Swainson's Hawk (*B. Swainsoni*; Sarasola & Jovani 2006), there is no experimental evidence as to how growth-bar width reflects dietary adequacy in Upland Buzzards. For our study, we assumed that growth-bar width is a valid indicator of the nutritional condition of this species.

In general, because of the importance of the plumage coat for protection and thermoregulation, feather generation should proceed as rapidly as possible, subject to constraints such as net energy intake. Net energy intake is dependent on the parental provisioning capability, sibling competition, and ambient temperature and precipitation. Reduction of feather growth might be considered as a compensatory mechanism counterbalancing such constraints. Thus, the reduced growth of a feather could indicate that nutritional condition is too low, causing catabolism of body tissues and mass loss. These two measures are generally considered the definitive indicators of nutritional stress (King & Murphy 1985, Yosef & Grubb 1992).

We tested three predictions, deduced from the above hypothesis, that food availability influences fledging success. (1) Prey availability will influence nestling growth which will be reflected in feather growth rates. (2) Brood size will influence individual nutritional condition (indicated by feather growth and fault bars, lengths of tarsus, culmen and 9th primary, and body mass). In other words, nestlings in larger broods will have comparatively smaller growth bars, suggesting increased sibling-competition resulting in reduced nutritional condition. (3) Hatching order will influence nutritional condition of the nestlings, i.e., the nestlings hatched first will be in better nutritional condition than subsequently hatched siblings.

2. Material and methods

Field work was conducted in 2007 during the breeding season (from May to August) of the Upland Buzzard in Central Mongolia, in two separate areas that had different densities of Brandt's Vole. Brandt's Vole densities were estimated following Batsaikhan *et al.* (2001), Avirmed (2003, 2005) and Gombobaatar (2006). We thus counted the number of wintering colonies in the spring (beginning of the breeding season) and in the summer (middle of the breeding season). We classified the areas as hosting abundant voles ("high-vole density area", HVDA) and no voles ("no-vole area", NVA).

During the breeding season, we sought active Upland Buzzard nests and re-checked known nests from previous years. Each active nest was rechecked 2–8 times during the breeding season. We measured certain biometrics (culmen, 9th primary, tarsus, body mass) of 59 nestlings in 22 nests within 7 days of hatching. We also measured 15 nestlings in 8 active nests in the no-vole area. We clipped a rectrix (R5) of each nestling when they were between 42–50 days old. Feathers were stored in disinfected Ziplock bags and brought to the Ornithological Laboratory of the National University of Mongolia in Ulaanbaatar. All feathers were collected and coded by GS and OB so that RY could measure them in a "blind" fashion without knowing from which clutch or habitat they had been taken.

Descriptive statistics for analyzing data of feather growth-bar length, number of fault bars, growth of culmen, primary (P9), tarsus and body mass increase was used. Regression analysis was used to evaluate statistical differences between average length of growth bar, number of fault bars and the number of nestlings in HVDA and in NVA, and also between growth bars and average length of bill, primary (P9), tarsus and weight. A single-factor ANOVA was used to evaluate the similarity of these nestling measures between HVDA and NVA (Krebs 1989). We used Jump 5.0 and MS Excel 2003 software to carry out all statistics.

3. Results

3.1. Hatchling numbers in HVDA and NVA

During the study year, the average clutch size in HVDA was 4.1 ± 1.2 SD (variation 2–7; $n = 22$) and in NVA was 2.8 ± 0.8 SD (2–4; $n = 8$). Likewise, the number of nestlings was on average higher in HVDA than in NVA, being 3.8 ± 0.8 SD (1–5; n = 60) and 2.4 ± 1.1 SD (1–4; $n = 15$), respectively. The average daily growth-bar width and the number of nestlings within the brood significantly and negatively correlated in HVDA ($R^2 = 0.74$, $R = 0.9$, $F = 12$, $P = 0.04$) but not in NVA ($R^2 = 0.42$, $R = 0.6$, $F = 2.9$, $P = 0.186$) (Fig.3).

Between HVDA and NVA, there was a marginally significant difference between the number of hatchlings comprising the brood in a given nest, and in the daily growth rate of culmen (ANOVA; $F_{3,53} = 2.8$, $P = 0.07$), but not in the growth rate of 9th primary ($F_{3,54} = 2.8$, $P = 0.3$) or tarsus ($F_{3,54} = 2.7$, $P = 0.2$).

3.2. Hatchling body condition in HVDA and NVA

The average width of growth bars was significantly wider in the HVDA than in the NVA ($F_{1,73} = 3.9$, $P < 0.0001$; Fig. 2). In the HVDA, the average was 3.9 ± 0.5 SD mm and variation was 2.8–5.3 mm ($n = 60$) and in the NVA the average was 2.24 ± 0.3 SD mm, variation being 1.74–3.01 mm ($n = 15$). Similarly, there was a significant difference between the average number of fault bars in the feathers of the nestlings ($F_{1,73} = 3.97$, $P = 0.0002$). The number of fault bars was greater in the HDVA (2.2 ± 2.1 SD, variation 0–12 $n = 60$) than in the

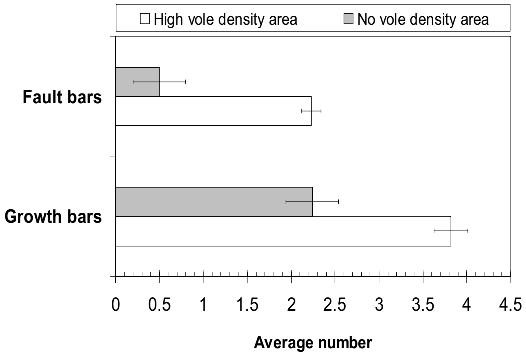

Fig.2. Average growth bar lengths and numbers of fault bars in nestling Upland Buzzards in high-vole-density and no-vole areas in Mongolia.

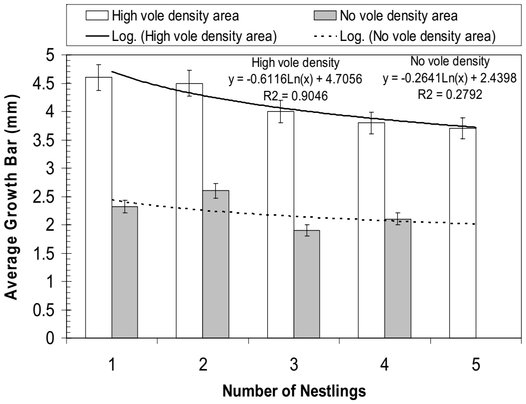

Fig.3. Average growth-bar width and the number of nestlings of Upland Buzzard in the high-vole-density and no-vole areas in Mongolia.

NVA 0.5 ± 0.7 SD (variation 0–2, $n = 15$; Fig. 2).

The nutritional condition of the first-hatched nestlings was almost always superior to that of the subsequently hatched siblings in both the HVDA and the NVA. In the HVDA, the average growth-bar width for the first hatchling was 4.16 ± 0.88 SD ($t = 49.02$, 3.95–4.33 95%CI, $n = 60$). This measure decreased by on average 0.25 (variation 0.15–0.35) in each subsequent hatchling (Table 1a). In the NVA, on the other hand, the average growth-bar width for the first hatchling was 2.21 ± 0.15 SE mm, and this measure decreased by 0.15 ± 0.02 SE mm (Table 1b).

The daily body-weight increase of the first hatchling was 2.17 ± 0.12 g in the NVA, compared to 3.90 g in the HVDA (Table 2a). However, from the second nestling and henceforth, the decrease in nutritional condition was similar, being 0.24 ± 0.04 SD g, in both habitats, and each subsequent nestling was on average 0.24 g smaller than its immediately older sibling. To better understand the inter-sibling competition, we checked for the possible effect of clutch size on the nutritional condition of the nestlings but found no significant effect of clutch size after correcting for the hatching order (Table 2b). The number of fault bars and the brood size exhibited a significant positive correlation in the HVDA ($R^2 = 0.97$, $R = 0.98$, $F = 148.3$, $P = 0.001$) but not in the NVA ($R^2 = 0.2$, $R = 0.3$, $F = 3.3$, $P = 0.2$) (Fig.4).

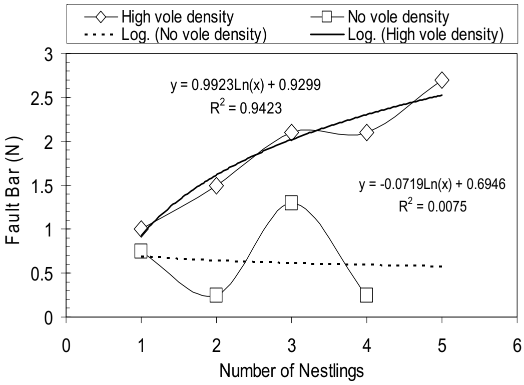

Fig.4. The number of fault bars as a function of brood size in Upland Buzzards in Mongolia.

3.3. Potentially available food

The average Brandt's Vole density was 441.6 ind/ha in the HVDA, whereas we found no vole colonies in the NVA (estimates based on 18 plots; see Material and methods). We observed that the broods located in the midst of HVDA were almost exclusively fed on voles and only occasionally other small rodents. In contrast, broods in the NVA were provisioned with a wider range diet that included fledglings of passerines (Isabelline Wheatear *Oenanthe isabellina*, Père David's Snow Finch *Pyrgilauda davidiana* and Horned Lark *Eremophila alpestris*), small mammals (Mongolian Gerbil *Meriones unguiculatus*, Campbell's Hamster *Phodopus campbelli*, Daurian Ground Squirrel *Spermophilus dauricus*), reptiles (Mongolian racerunner *Eremias argus*) and occasionally larger mammals (Daurian Hedgehog *Mesechinus dauuricus* and Tolai Hare *Lepus tolai*).

Table 1. The effect of hatching rank within a clutch of the Upland Buzzard in (a) high-vole-density area (HVDA; Eej Khad), and (b) in areas with no voles (NVA; Desert Steppe) in Mongolia.

a. High-vole-density area

Parameter	Estimate	SE	*t*	*P*	95%CI
Intercept	4.16	0.085	49.02	<0.0001	3.990…4.330
Ranking	–0.25	0.048	–5.20	<0.0001	–0.346…–0.154

b. No-vole areas

Parameter	Estimate	SE	*t*	*P*	95%CI
Intercept	2.21	0.150	14.80	<0.0001	1.860…2.567
Ranking	–0.15	0.022	–6.77	0.0005	–0.206…–0.097

Table 2. (a) The effect of study area (high-vole-density or no-vole areas; HVDA or NVA, respectively) on the nutritional condition of Upland Buzzard nestlings. (b) The effect of clutch size on the nutritional condition between clutches of the Upland Buzzard.

a. Average nutritional condition

Effect	Estimate	SE	df	*t*	*P*
Intercept	2.17	0.121	23	17.93	<0.0001
Habitat (HVDA)	1.73	0.132	2	13.10	0.0058
Habitat (NVA)	0.00				
Ranking	–0.24	0.039	49	–6.22	<0.0001

b. Clutch-size effect

Effect	Estimate	SE	df	*t*	*P*
Intercept	4.54	0.234	17	19.42	<0.0001
Ranking	–0.25	0.045	40	–5.48	<0.0001
Clutch size	–0.04	0.067	17	–0.54	0.5937

4. Discussion

Our results demonstrate, for the first time, that the nutritional condition of broods located in areas with abundant Brandt's voles appeared better than areas with no or a scarcity of voles, if estimates are based on feather growth-bar length. However, these two habitat types did not significantly differ in terms of the number of fault bars. Thus, even though growth-bar width may be wider and correlate with prey density or consumption, the number of fault bars may not necessarily be lower, as has been assumed to date. The latter assumption was the result of several studies showing that individuals with wider growth bars also tended to have lower number of fault bars (e.g., Yosef 1996, Yosef & Grubb 1992) or, alternatively, that the feathers were longer and heavier (e.g., Waite 1990, Jenkins *et al.* 2001). Our finding thus suggests that resources affecting fault bars may not necessarily represent nutritional condition per se; in other words, either growth bars or fault bars in any bird do not have to be inter-connected, or that other extrinsic and/or intrinsic factors can influence them. However, further studies on the external factors and physiological mechanisms that can independently influence growth and fault bars are needed to reach a better understanding of the intimate relationship between diet quality and abundance, and the true nutritional condition of raptor individuals.

Fault bars are still poorly understood and considered to result from reduced nutritional condition (Slagsvold 1982, Machmer *et al.* 1992, Yosef 1996, Yosef & Grubb 1992) and stress-related episodes (King & Murphy 1984, Negro *et al.* 1994). Jovani and Blas (2004) found that the probability of formation of fault bars is lowered in an adaptive way in those feathers that require more strength during flight, and called it the "fault bar allocation hypothesis." Similarly, Sarasola and Jovani (2006) supported the theory but suggested that the selection pressure could be relaxed in other instances, leaving the way free for other mechanisms that would influence fault bar occurrence.

In our case it is possible that, because the HVDA broods were fed only readily available voles, this could have nutritionally disadvantaged them, as selectively evidenced in fault but not in growth bars. Perhaps the higher prey abundance allowed breeding pairs to raise larger broods, which, however, does not mean that these larger broods are in better nutritional condition. The hatchlings of large broods could have a greater number of fault bars owing to increased sibling competition. This hypothesis is corroborated by the fact that, although the nutritional condition of the individuals hatched first was always superior to that of subsequently hatched siblings in both HVDA and NVA habitats, from the second nestling onward, the decrease in nutritional condition was the same. In both habitats each subsequent nestling was on average 0.24 g smaller than its immediately older sibling, which indicates that body condition is a function of hatching rank (Table 2a). This relative decrease in nutritional condition between siblings was constant in both habitats, and the trend was independent of prey abundance. The average growth-bar width for the first hatchling in the high-vole-density area – i.e., on the grassland steppe – was 4.16 mm and each subsequent fledgling decreased by 0.25 mm (Table 1a). Similarly, in the no-vole area – desert steppe, with no detected vole colonies – the average growth-bar width for the first hatchling was 2.21 and for each subsequent sibling decreased by 0.15 mm (Table 1b).

A comparison of the average daily growth-bar width growth and the number of nestlings within the brood, resulted in a significant and negative correlation in HVDA but not in NVA (Fig. 3). We consider parental investment to have played an important role in nestling food intake. We did not study the behavior of the parents at the nest nor their role in food allocation to the nestlings, but the fact that there is a difference between siblings in high-vole-density area but not in the desert steppe (NVA) suggests a change in their attitude towards the brood. The breeding birds in HVDA may not have considered food allocation to be of importance owing to its abundance. This may have resulted in the older siblings eating a larger portion of the food brought to the nest, in turn resulting in a disparity in body size and nutritional condition between early- and late-hatched individuals in the brood. In a study on Starlings (*Sturnus vulgaris*), Kacelnik *et al.* (1995) postulated that although the effect of begging on the feeding probability may be mediated by parental choice, the effect of position depended on between-chick dynamics, with the parents apparently accepting the outcome of these interactions. Also, Scott Forbes (2004), who studied food sharing among nestlings of facultatively siblicidal Ospreys (*Pandion haliaetus*), found that feeding among brood members was hierarchical: senior dominant siblings ate more when hungry, leaving a smaller residual share of food for junior siblings. He discovered that aggression was infrequent and food allocation was skewed toward the junior sibling in broods with artificially exaggerated hatching intervals, suggesting that senior siblings were less aggressive when their dominant status was not threatened.

In contrast, the difference in growth rate between siblings in NVA was not great, suggesting that it is not influenced by between-sibling competition, but instead another factor regulated growth rate. If this is the case, then parental care must play an important role, whereby the feeding parents allocate prey evenly to all the nestlings. Wright *et al.* (1998) suggested that, when faced with increased brood demand, parent birds provisioning young in the nest make a variety of adjustments to their foraging and food-allocation strategies. They found that although European Starling chicks in large and small broods showed similar food intake rates, there was an adaptive significance of the provisioning trade-off between quality and quantity of food. This was related to natural variation in foraging conditions and brood demand. This behavior has been previously suggested for differences in breeding success between two populations of the

Common Buzzard (*Buteo buteo*) in Scotland (Swann and Etheridge 1995). However, such a line of thought should be considered with caution because Potapov (1997) found that, although the density and clutch size of breeding Rough-legged Buzzard (*Buteo lagopus*) in the Siberian tundra was correlated with small mammal population density, the most accurate regression model to predict the overall reproductive output included only the rate of change in the small mammal diversity. He found that the number of offspring produced by the buzzards in a given area fluctuated synchronously with the small-mammal density, but the cycle was significantly more consistent in amplitude in the predator as compared to the prey.

To better understand the inter-sibling competition, we checked for the possible effect of clutch size on the nutritional condition of each of the nestlings in every brood included in the study. There was no additional effect of clutch size after correcting for the hatching rank (Table 2b). This finding substantiates our conclusion that inter-sibling rivalry results in reduced nutritional condition of the younger siblings but not in the number of young in the brood. Overall, the nutritional condition appeared lower in desert-steppe areas (NVA), but the effect of clutch size was weaker on each subsequent nestling there than in the high-vole-density Eej-Khad area (HVDA). However, owing to a small sample size in the desert steppe ($n = 8$) we were unable to substantiate this finding statistically.

High vole densities apparently allow Upland Buzzards to lay larger clutches and fledge more young; indeed, in the present study the average clutch size was 4.1 in HVDA but only 2.8 in NVA. Subsequently, hatching success and brood size was also higher in HVDA than in NVA (3.8 vs 2.4). These findings are similar to the predator-prey link between Montagu's Harrier (*Circus pygargus*) and common vole (*Microtus arvalis*) in France (Salamolard *et al.* 2000).

However, the number of fault bars on the feathers and the size of broods delivered a different message. We found that there was a significant positive correlation between these factors in HVDA but not in NVA. Based on body weight increase, the nutritional condition of all the nestlings was lower in the latter (Fig. 4). The number of fault bars found in HVDA suggests that, as with the growth-bar width, the hatching rank influences the relative nutritional condition of the siblings within the clutch. The first-hatched individual was always in better nutritional condition, as evidenced by the lower number of fault bars and wider growth bars. Each subsequent sibling, in order of hatching, appeared nutritionally disadvantaged, as evidenced by their smaller growth bars and more numerous fault bars. With as much as 24h between siblings, this is most probably the consequence of the eggs hatching asynchronously. Compared to the youngest siblings, older ones are stronger and better able to fend for themselves when parents bring food to the nest. On the other hand, in NVA, the lack of food in the desert did not show any trend (Fig. 4). This finding is of interest because it suggests that the provisioning capabilities of each pair influence the nutritional condition of the brood independent of habitat and prey abundance. However, of greatest interest is the fact that the number of fault bars, which suggests the number of days of stress resulting in insufficient keratin laid on the feather, was greater in HVDA and was true for all nests irrespective of brood size. This appears to be contradictory to present wisdom, but can be explained by the relative growth rates of the nestlings in the two habitats.

There was no significant difference between the number of nestlings and the daily growth of bill, 9th primary and tarsus length. However, there was a significant difference between the number of nestlings and the rate of daily weight increase of nestlings in HVDA. Hatching rank did not affect the daily growth rate in HVDA but was one of the causes of differential daily growth rate in NVA.

In conclusion, ptilochronology can be an effective method to evaluate the relative nutritional condition of nestlings of the Upland Buzzard. However, in future studies the feather growth rate, feather weight, growth-bar width, and fault bars must be evaluated in an independent basis and not considered as a common parameter to elucidate the bigger picture. It is of great interest to tease apart the natural selection processes whereby the occurrence of fault bars is reduced in areas where they can be detrimental to the birds' survival.

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Mongolianaromyyrän kannantiheys vaikuttaa mongolianhiirihaukan ravitsemustilaan mongolialaisella ruohoarolla

Tutkimme mongolianhiirihaukan (*Buteo hemilasius*) ravitsemustilaa käyttämällä sulkien kasvuun perustuvaa ptilokronologiamenetelmää. Menetelmä perustuu siihen, että sulan yksi kasvujuova vastaa 24 tunnin kasvua; kasvujuovien leveyttä käytetään ravitsemustilaa kuvaavana indeksinä. Vaikka menetelmää on käytetty päiväpetolinnuilla, mongolianhiirihaukalla ei ole kokeellisesti osoitettu kasvujuovien leveyden kuvaavan ravitsemustilaa.

Kenttätyöt tehtiin pesimäkaudella 2007 Keski-Mongoliassa kahdella alueella, jotka erosivat mongolianaromyyrän (*Lasiopodomys brandtii*) kannantiheyden suhteen. Myyrälaji on mongolianhiirihaukan pääravintoa. Kahdeksassatoista näytteenottopisteessä Eej Khadin alueella myyrätiheys oli 441,6 yksilöä/ha, kun taas aavikkoarolla tiheys oli nolla. Pesäpoikasten kasvujuovat kasvoivat nopeammin myyrärikkaalla kuin myyrättömällä alueella (3,9 vs 2,24 mm/24 tuntia). Valejuovien kasvu oli vastaavasti 2,2 ja 0,5. Saaliin (myyrien) runsaus vaikutti myös pesyekokoon, mikä oli korkeampi myyrärikkaalla alueella (4,1 vs 2,8), mikä edelleen johti korkeampaan lentopoikasten määrään (3,8 vs 2,4).

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