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SIBLING COMPETITION INDUCES STRESS INDEPENDENT OF NUTRITIONAL STATUS IN BROODS OF UPLAND BUZZARDS

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ABSTRACT.—In any evaluation of the health and well-being of wildlife, whether to test biological theory or evaluate conservation problems, it is imperative to know to what degree variables are operating independently. Too often, important ecological and physiological traits such as body mass, immune function, and blood parameters may have a common agent influencing them; one example is glucocorticoids (corticosterone in birds) secreted in response to environmental stressors. We evaluated the nutritional condition of broods of Upland Buzzards (*Buteo hemilasius*) in Mongolia using ptilochronology, a measure of growth rate of feathers, and the amount of corticosterone in feathers as a long-term integrated measure of the response to stressors. Absolute amount of feather corticosterone was not significantly related to food supply, attributes of the brood, or feather growth rate. However, the relative amount of corticosterone of junior nestlings vs. their senior siblings increased as the age difference between them increased. Similarly, in the study area with larger broods where more sibling competition likely existed, junior siblings showed relatively higher amounts of stress. Our results suggested that stress seemed to be associated with sibling conflicts, and not a product of the consequences of the nutritional condition of the individuals.

KEY WORDS: *Upland Buzzard*; Buteo hemilasius; *corticosterone*; *Mongolia*; *nutritional condition*; *ptilochronology*; *sibling competition*; *stress*.

LA COMPETENCIA ENTRE HERMANOS INDUCE ESTRÉS INDEPENDIENTEMENTE DEL ESTATUS NUTRICIONAL EN NIDADAS DE *BUTEO HEMILASIUS*

RESUMEN.—En cualquier evaluación de la salud y el bienestar de la vida silvestre, si se quiere probar una teoría biológica o evaluar problemas de conservación, es imperativo conocer hasta qué grado las variables están operando independientemente. Muy a menudo, atributos ecológicos y fisiológicos importantes como la masa corporal, la función inmunológica y los parámetros hematológicos pueden tener un agente común que los influencia. Un ejemplo de ello son los glucocorticoides (corticosterona en las aves) segregados en respuesta a un factor de estrés ambiental. Evaluamos la condición nutricional de nidadas de *Buteo hemilasius* en Mongolia usando la ptilocronología, una medida de la tasa de crecimiento de las plumas, y la cantidad de corticosterona en las plumas como una medida integrada a largo plazo de la respuesta a los factores de estrés. La cantidad absoluta de corticosterona en las plumas no estuvo relacionada significativamente al suministro de alimento, atributos de la nidada o la tasa de crecimiento de las plumas. Sin embargo, la cantidad relativa de cortisona de pichones jóvenes vs. pichones más viejos se incrementó a medida que la diferencia de edad entre ellos aumentó. De manera similar, en el área de estudio con nidadas más grandes, donde es probable que exista una mayor competencia entre hermanos, los pichones más jóvenes evidenciaron cantidades relativamente mayores de estrés. Nuestros resultados sugieren que el estrés parece estar asociado con los conflictos entre hermanos y que no son un producto de las consecuencias de la condición nutricional de los individuos.

[Traducción del equipo editorial]

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Sibling competition within broods, especially for raptors, varies with size hierarchies created by hatching asynchrony, and its consequences are often poor growth and high mortality of the youngest nestling (e.g., Bortolotti 1984, Wiebe and Bortolotti 1994). Older nest mates may indirectly influence the demise of their younger sibling through better competitive ability, or may directly do so through aggression (Mock 1984). Food availability in the nest is often not a proximate cue for sibling aggression (e.g., Mock et al. 1987). Therefore, immediate food supply may not be the reason why the youngest nestling fails to thrive (Newton 1998). We hypothesized that physiological stress may either be associated directly with food supply, or with the nature of sibling competition independent of food quantity. In the latter case, size hierarchies within a brood determine the degree to which the oldest nestling can dominate its youngest sibling. Ptilochronology is a tool for studying the nutritional condition of birds and is well established as a tool for a wide range of applications in avian research (Grubb 1989, 1991, 1995). Growth bars are the dark and light bands on the vane that are produced during the day and night, respectively, such that each pair of bars represents 24 hr of feather growth. Growth bars show a direct relationship with nutritional condition (Hill and Montgomerie 1994, Yosef 1997, Carrascal et al. 1998, Jenkins et al. 2001), territory quality (Yosef and Grubb 1992, Stratford and Stouffer 2001), plumage color (Hill and Montgomerie 1994), reproductive effort and social dominance (White et al. 1991, Grubb et al. 1998), biometry (Polo and Carrascal 1999), habitat quality and choice (Hogstad 1992, Grubb and Yosef 1994, Yosef 1997, Carlson 1998), susceptibility to stress (Machmer et al. 1992, Yosef and Grubb 1992, Bortolotti et al. 2002, Gombobaatar et al. 2009), flocking vs. floaters (Grubb and Cimprich 1990, Hogstad 2003), and caching or supplemental feeding (Grubb and Cimprich 1990, Waite 1990, Brodin and Ekman 1994).

Fault bars are still poorly understood and considered to result from reduced nutritional condition (Slagsvold 1982, Machmer et al. 1992, Yosef 1997, Yosef and Grubb 1992) and stress-related episodes (King and Murphy 1984, Yosef and Grubb 1992, Negro et al. 1994, Jovani and Diaz-Real 2012). 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, allowing other mechanisms to influence fault bar occurrence.

In a recent study of the Upland Buzzard (*Buteo hemilasius*), Gombobaatar et al. (2009), used ptilochronology to evaluate the relative nutritional condition of nestlings and showed that inter-sibling rivalry resulted in reduced nutritional condition of the younger siblings but not in the number of young in the brood. However, they were unable to explain why the number of fault bars, an indicator of exposure to stressors, was greater in broods in areas of high prey density irrespective of brood size. These results were particularly puzzling as it has generally been assumed that nutritional condition and stress vary together (Grubb 2006). They suggested that sibling rivalry, wherein the older and larger siblings dominated the younger and weaker nestlings, was responsible for the higher incidence of stress, even when there was a surplus of food supplied by the parents. However, they were unable to substantiate this hypothesis. Although ptilochronology allows the researcher to evaluate the nutritional condition of the individual on a daily basis by measuring the growth bar, and the frequency of some stressors are recorded by the presence of fault bars (Bortolotti et al. 2002, Jovani and Diaz-Real 2012), it is desirable to know how a bird responds physiologically to the potentially numerous events and periods of stress (i.e., noxious stimuli that challenge homeostasis) in their lives. This can best be determined by evaluating endocrine function.

When faced with environmental pressures that result in stress, the vertebrate hypothalamic–pituitary–adrenal (HPA) axis responds by releasing circulating glucocorticoids, which elicit a suite of behavioral and physiological changes known as the stress response (Sapolsky et al. 2000). This response is known to redirect animals to a life-saving state, allowing them to overcome stress and reestablish homeostasis in the best possible physical condition (Wingfield and Ramenofsky 1999, Wingfield and Silverin 2002). Measuring the response to stressors over a long time frame has recently been made possible with the advent of a technique whereby corticosterone (CORT) is extracted from feathers (Bortolotti et al. 2008, 2009a). Feathers are a long term and stable record of physiological processes. Although dead upon maturity, the cells of a growing feather are highly vascularized and numerous compounds which have no function in mature feathers

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(e.g., heavy metals, trace elements, xenobiotics) are deposited in the keratin structure (Bortolotti and Barlow 1988, Dauwe et al. 2003, Bortolotti 2010).

In this study, we measured the amount of immunoreactive CORT deposited in feathers of nestling Upland Buzzards (the same individuals measured in Gombobaatar et al. 2009), as an historical record of each nestling's HPA activity during the weeks of feather growth in the nest. These measurements integrate different aspects of HPA activity, including the frequency and magnitude of response to stressors and, to a lesser degree, variation in baseline levels (see Bortolotti et al. 2008, 2009a). Our objective in this study was to combine the widely used technique of ptilochronology (e.g., Bujoczek et al. 2011) with the novel technique of analyzing feather CORT (e.g., Bortolotti et al. 2008), and determine whether this long-term measure of stress hormone can provide a valuable perspective on the ecophysiology of individual birds. We also examined how, under natural conditions, feather CORT may shed light on the phenomenon of sibling competition.

METHODS

Study Species and Study Area. The Upland Buzzard is a monotypic species whose breeding distribution is confined to the eastern Palearctic (ca. from 53° to 30°N). The majority of the core population occurs 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 and Christie 2001, Gombobaatar 2010). In Mongolia, the Upland Buzzard breeds from the Altai Mountains to the western foothills of the Great Khyangan Mountains (Flint and Bold 1991). Our study areas were in central Mongolia, in two separate areas that had dramatically different densities of Brandt's vole (*Lasiopodomys brandtii*; see Gombobaatar et al. 2009, 2010).

Morphometrics and Feather Collection. During the 2007 breeding season (May to August), we measured biometrics (culmen, 9th primary, tarsus, body mass) of 59 nestlings in 22 active nests in a high vole-density area and 15 nestlings in eight active nests in an area with essentially no voles. We clipped one rectrix (R5) of each nestling at age 42–50 d old. Ptilochronology and CORT extraction were conducted blind to study area (Gombobaatar et al. 2009), but we were able to extract CORT from only 44 of the feathers, from 22 nests. This resulted in the sample sizes of 47 nestlings from 18 nests in the high vole-density area and 14 nestlings from eight active nests in the low-density habitat.

Feather Analysis. We extracted CORT from feathers using a methanol-based extraction technique (see Bortolotti et al. 2008, 2009a) at the Department of Biology, University of Saskatchewan (Canada). Data are expressed as pg CORT per mm, not per mg, of feather. The reason for doing so involves the nature of CORT deposition in feathers: CORT is deposited per unit time of feather growth which is approximated by length (also see Bortolotti 2010). We assessed the extraction efficiency by including feather samples spiked with a small amount (approximately 4000 DPM) of 3H-corticosterone (for more details about feather extraction see Bortolotti et al. 2008). Greater than 98% of the radioactivity was recoverable in the reconstituted samples. The within-assay variability was 7.3%. We assessed detectability using the E.D. 80 value, and all our samples were well above the estimated 10.15 pg per tube.

For some analyses we compared junior to senior nestling in the same brood. This varied from being nestling 1 vs. nestling 2 to nestling 1 vs. nestling 5. $P < 0.05$ was considered the minimum level of significance.

Statistical Analyses. Initially, we applied generalized linear mixed models with normal-type error distribution with an identity-link function (GLIMMIX, SAS 9.2). We used feather CORT as the dependent variable, and the independent variables were nest (random factor), area (fixed factor), brood (fixed factor), nestling position in brood (fixed factor), and ptilochronology (covariate). If growth bars are in fact correlated with stress, then the hypothesis that stress is associated with environmental variables that influence nutritional condition should hold; however, the result was that all independent variables were not statistically significant ($r^2 = 0.001$ for all tests). We then tested the hypothesis that as disparity of size between siblings increases, the junior nestling within a brood suffered increasing stress, using the same variables as specified before.

RESULTS

Mean CORT levels differed little between first- and second-hatched siblings but increasingly grew in siblings hatched later (Fig. 1). The result, although not statistically significant ($r_s = 0.474$, $P = 0.074$; $n = 15$) was suggestive of a trend, and we consider that this may be a result of our limited sample size.

As most of the small broods were from the no-vole area (average brood size 2.8 ± 0.8 nestlings (range = 2–4, $n = 8$ vs. the high vole-density area: 4.1 ± 1.2 nestlings, range = 2–7, $n = 22$), we could not separate an effect of area ($F_{1,13} = 4.91$, $P = 0.045$) from

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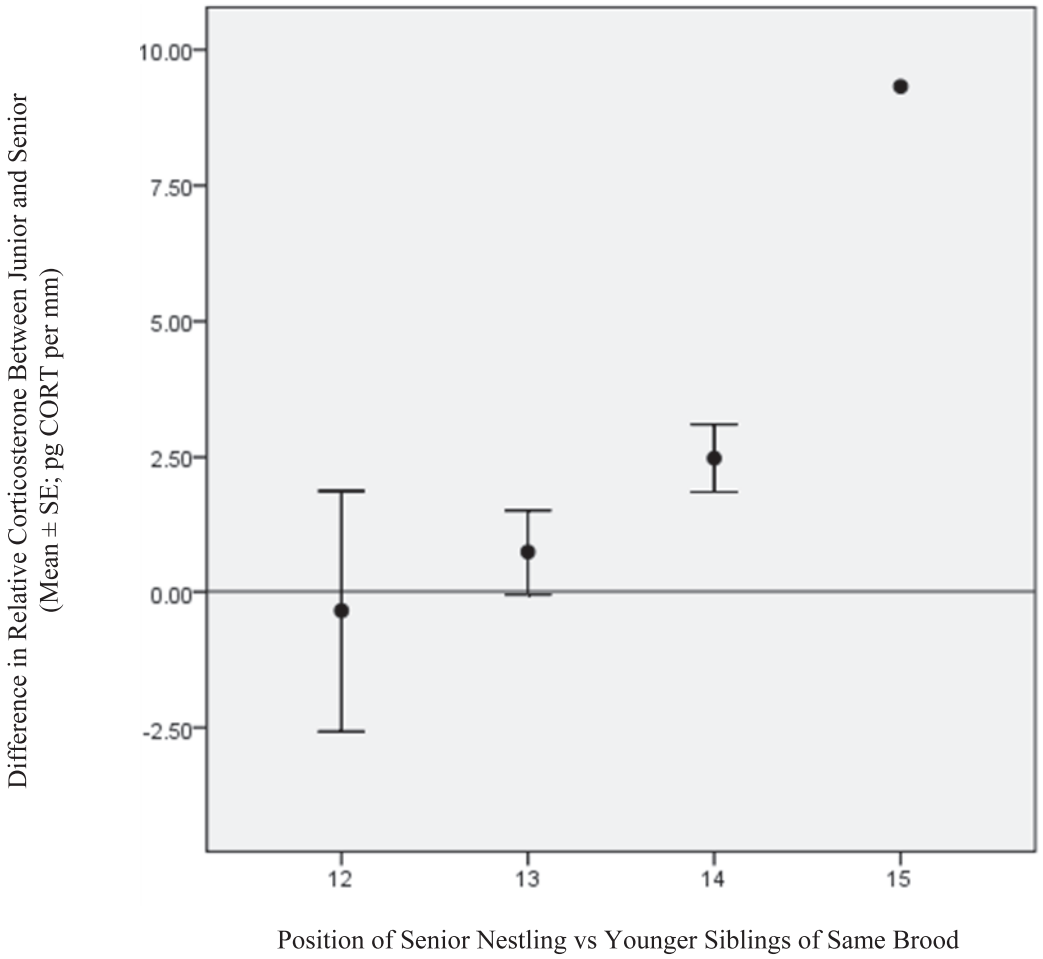


Figure 1. Relative corticosterone levels versus the brood position of the junior nestling. First and second nestlings (n = 16) are similar in values, but younger and smaller junior nestlings display increasing levels of corticosterone (n = 19 third nestlings, n = 8 fourth nestlings; n = 1 fifth nestling).

an effect of sibling competition. We therefore conducted an ANOVA wherein CORT was the dependent variable while area and difference in relative growth of feather were independent variables. The result was that the difference in CORT between junior and senior siblings was greater in the high vole-density area ($F_{1,13} = 5.30$, $P = 0.040$), and as relative stress increased so did relative growth of feather ($F_{1,13} = 3.93$, $P = 0.090$).

DISCUSSION

Gombobaatar et al. (2009) concluded that ptilochronology may be an effective method to evaluate differences in nutritional condition among nestlings, but that future studies should also independently evaluate feather growth rate, growth bar width, and fault bars for a more complete understanding of nutritional status. Contrary to the previous assumption that growth bar width and the number of fault bars are linked (Grubb 2006), our results seemed to support the possibility that these variables have independent mechanisms: fault bars are indicators of stressful events whereas growth bars represent relative nutritional condition. Bortolotti et al. (2009b) corroborated this with the finding that fault bars were a localized area of high amounts of corticosterone in the feather. Vangestel and Lens (2011) also found a lack of relationship between ptilochronology and ''stress'' as evaluated by fluctuating asymmetry in House Sparrows (*Passer*

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domesticus). Jovani and Diaz-Real (2012) confirmed in White Storks (*Ciconia ciconia*) that one growth band represented 24 hr of feather regeneration, and that fault bars are a discrete event of a finite duration occurring mainly during the night. They concluded that acute stressors, rather than chronic ones, were responsible for fault bar formation. Hence, although our study seems to support the fault bar analysis of the initial study (Gombobaatar et al. 2009), it more importantly provides a unique perspective on stress. Junior nestlings may have suffered from conflicts with their older and larger siblings, rather than stress being the result of lack of food. The fact that broods were larger in areas with abundant prey revealed that the fledging of a large number of young might not necessarily be as beneficial as it would seem, as the smallest nestlings' chance of survival may be reduced right from the beginning. Inversely, as the CORT levels and number of fault bars were reduced in small broods, sibling competition was lower in nestlings whose nutritional condition was relatively poor. It is still unclear what portion of the poor probability of post-fledging survival, so typical of youngest members of the brood in asynchronously hatched birds, can be ascribed to poor food resources vs. the negative impacts of stressors such as sibling conflicts.

Many physiological processes are characterized by great variability among individuals, something that ecophysiologists attempt to elucidate (cf. Bortolotti et al. 2009b, Jovani and Diaz-Real 2012). Our study provides an index, the production of corticosterone, which is indicative of responses to environmental perturbations, to help illuminate why individuals are more or less likely to thrive during the critical initial stages of their life—the nestling and fledging stages. Although the sample size was limited, we showed that feather CORT and width of feather growth bars were independent variables, and that patterns of CORT were consistent with those for fault bars. Because the relative stress was unrelated to nutrition, we concluded that stress of sibling conflicts may have been causal. Such information is crucial if we are to understand how or where selection influences individual survival.

From a conservation standpoint, the coupling of ptilochronology and evaluation of feather CORT, especially for endangered species for which invasive techniques are discouraged, may assist in decisions concerning resource management and brood-size manipulation.

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