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Post-natal Growth of the Formosan Reeves' Muntjac *Muntiacus reevesi micrurus*

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Kurtis Pei (1996) Post-natal growth of the Formosan Reeves' muntjac *Muntiacus reevesi micrurus*. *Zoological Studies* **35**(2): 111-117. A total of 383 Formosan Reeves' muntjacs *Muntiacus reevesi micrurus* were examined during December 1988 and January 1989 in Ilan, Taiwan. All specimens were aged according to their tooth eruption or the wear pattern of the 1st lower molars. Growth of the mandibular diastema showed no difference between the 2 sexes, and the maximum length was reached shortly after 1 year of age. Body growth ceased at about 2 years of age in females, while males continued growing beyond 2 years of age. In adults (> 2 years old), males were significantly heavier than females (means = 8.3 and 6.8 kg, respectively). The heavier body weight is considered a reflection of the dominant status of males over females. The length of the canine teeth in males continued to grow until males were 2 to 3 years old, but broken canines were commonly found in adult males.

Key words: Body weight, Cervidae, Canine teeth, Growth curves, Sexual dimorphism.

Growth, in physiological terms, can be considered a process of accumulation and development of body tissues that occurs when the rate of anabolism exceeds the rate of catabolism. Since the growth of individuals, in addition to reproduction and immigration, represents a major part of population production (Sinclair 1977), knowledge of the various features of growth is fundamental to unraveling the dynamics of a population. On the other hand, because growth patterns during ontogeny generally reflect evolutionary adaptations to the organism's environments, understanding the general patterns of growth is also helpful in elucidating the life history of a certain species (Wilbur and Collins 1973, Robbins and Robbins 1979, Atchley 1984, Chesser and Smith 1987).

In the case of the Indian muntjacs (*Muntiacus muntjak*), a number of measurements at birth (i.e., body weight, total body length, and shoulder height) have been given (Sankhala and Desai 1969, Acharjyo 1970, Acharjyo and Misra 1972, Walker 1975, Acharjyo and Mishra 1981). Similar data are available for the Reeves' muntjac (*M. reevesi reevesi*: Dansie 1970, Talbot 1980). However, with the exception of the development of dentition and sexual maturation (e.g., Chapman et al. 1985, Pei and Wang 1991, Pei et al. 1991, Pei and Liu 1994), patterns of post-natal growth in muntjac have not been extensively studied. The rate of weight gain for Reeves' muntjac was estimated at about 460 g/week during the first 6 to 8 weeks after birth (Dansie 1970), and the relationship between age and skull growth in the Formosan Reeves' muntjac was recently described by Wang (1989).

This paper describes the relationships of eviscerated body weight, length of the mandibular diastema, and length of the male's upper canines to age for the Formosan Reeves' muntjac.

MATERIALS AND METHODS

A total of 383 Formosan Reeves' muntjacs was trapped by aborigines from the Jiou-Jeng-Yang area, Ilan County, Taiwan, R.O.C. (24°27′0″N, 121°31′0″E) and were examined within 2 days after death during December 1988 and January 1989. Eviscerated body weight of each specimen

was determined with a Nagada model C-3 30-kg capacity spring scale to the nearest 0.1 kg. Lengths of each juvenile's mandibular diastema and male's upper canines were measured to the nearest 0.5 mm. The age of each specimen was estimated according to the tooth eruption (Chapman et al. 1985) or the wear pattern of their 1st lower molars (Pei and Wang 1991).

Three basic mathematical models, Logistic, Gompertz, and von Bertalanffy equations, were calculated separately to obtain the best-fitted growth curve for each growth parameter. However, since the r^2-value for the 3 models for all parameters were very similar, indicating that the variances explained by these models were the same, only the Logistic model is presented in this paper. Every specimen was considered to represent the mid-point of the age-class to which it belonged and the average of the measurements for each age-class was used in the calculation (Table 1).

The procedures for fitting a mathematical model to the data followed that described by Ricklefs (1967), and the formula of the Logistic model is:

$$W \text{ or } L = a/[1 + e^{-k(t-to)}]$$

in which **W** is mean weight (kg) at time **t**; **L** is mean length (mm) at time **t**; **a** is the asymptotic (or final) weight or length; **k** is a constant that is proportional to the slope on the inflection point of the growth curve, and which can be considered to be the coefficient of the overall growth rate (Brody 1945, Ricklefs 1967, Smuts et al. 1980); t is age in weeks; and **to** is the age at the inflection point. Biologically, **to** can be interpreted as the time when the growth shifts from the self-accelerating phase into the self-retarding phase (von Bertalanffy 1960, Monteiro and Falconer 1966, Batt 1980).

Table 1. Age and sex-specific mean and standard deviations (SD) of the eviscerated body weight, mandibular diastema length, and male's upper canine length for the Formosan Reeves' muntjac

Age (weeks)	Eviscerated body weight (kg)						Mandibular diastema length (mm)						Male's upper canine length (mm)		
	Male			Female			Male			Female					
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
5	2.45	0.07	2	2.90	1.23	5	24.5	0.7	2	25.5	2.8	2	0.0	—	2
12	3.20	—	1	3.4	—	1	29.5	—	1	28.0	—	1	0.0	—	1
17	4.00	—	1	2.90	—	1	—	—	—	29.0	—	1	0.0	—	1
24.5	4.43	0.74	35	4.42	0.75	26	32.3	2.3	28	31.6	2.2	18	0.8	2.2	45
30	5.55	1.03	10	4.42	0.35	3	34.1	2.3	8	33.9	0.9	4	4.3	4.7	13
39.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
50.5	6.56	0.58	14	5.50	1.03	13	36.5	1.9	13	35.4	2.5	9	13.5	2.1	13
57.5	6.17	0.55	3	5.86	0.75	5	—	—	—	36.8	1.8	3	12.1	2.1	3
62	7.00	0.42	2	—	—	—	37.5	2.1	2	—	—	—	17.8	2.1	2
71	6.78	0.55	5	6.30	—	1	36.5	2.4	4	—	—	—	14.3	2.9	8
75.5	6.70	0.98	4	—	—	—	38.5	3.2	2	—	—	—	15.5	2.0	6
80.5	—	—	—	—	—	—	—	—	—	36.0	—	1	17.0	—	1
85	7.50	—	1	5.70	0.82	3	34.3	3.9	2	33.8	1.1	2	18.4	0.6	2
89	6.67	0.67	3	5.90	0.42	2	35.3	3.6	5	35.0	—	1	15.8	2.1	4
92	—	—	—	—	—	—	37.5	—	1	—	—	—	19.8	—	1
98.5	7.83	1.33	7	6.44	0.84	16	36.5	0.7	2	33.2	1.8	3	19.1	3.7	7
130	7.85	0.93	11	7.13	0.61	11	37.3	3.2	2	38.0	—	1	21.3	3.1	10
182.5	8.45	0.71	6	6.55	0.80	13							23.7	1.5	3
234.5	8.67	1.34	3	6.56	0.76	11							21.7	1.3	4
286.5	8.93	0.81	3	6.93	1.21	7							25.0	—	1
338.5	8.50	—	1	6.65	0.40	3									
390.5	—	—	—	7.85	0.21	2									

RESULTS

Body weight

The best-fitted growth curve for post-natal eviscerated weight is shown in Figure 1. The parameters of the equation are given in Table 2. The youngest specimens in the sample were estimated to be 3 to 7 weeks old, and their mean eviscerated weight was 2.5 ± 0.1 kg (n = 2) and 2.9 ± 1.2 kg (n = 5) for males and females, respectively. Rate of weight gain during the growing period was almost the same for both sexes (compare k-values in Table 2). The length of the growth period, however, differed slightly between the 2 sexes. In males, body mass increases continuously, although slowly, beyond 2 years of age and they probably do not reach adult weight until 3 years of age. In females, weight becomes asymptotic at about 2 years of age (Fig. 1).

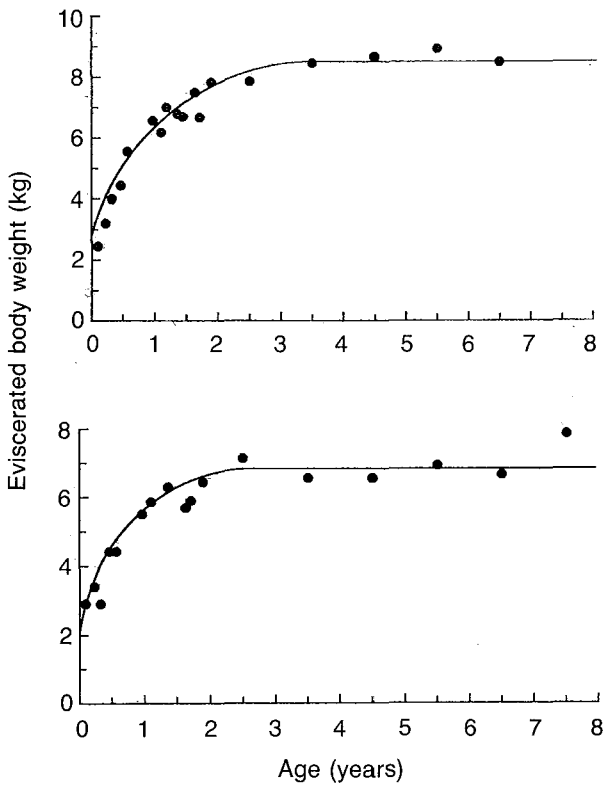

Fig. 1. Best-fitted Logistic growth curve for mean eviscerated body weight for male (top) and female (bottom) Formosan Reeves' muntjac *Muntiacus reevesi micrurus*.

The average eviscerated weight of males older than 2 years was 8.3 ± 0.9 kg (n = 24), and that for females was 6.8 ± 0.8 kg (n = 48). This difference is highly significant (t = 6.59; df = 70; $p < 0.0005$). The weight difference between sexes can also be seen from the values of the asymptotes (the theoretical final weight) determined for the best-fitted equations (Table 2).

Growth of the mandibular diastema

Unlike body weight, no significant difference was noted between the mean diastema lengths of males (36.5 ± 5.1 mm) and females (35.3 ± 2.2 mm) older than 1 year (t = 1.02; df = 52; $0.1 < p < 0.25$). Data for both sexes were therefore pooled. The growth plateau of the diastema is reached at a little over 1 year of age (Fig. 2).

Growth of male's upper canines

The upper canines of the muntjac have been reported to be the only teeth to show a sexual difference in time of replacement and size to which the permanent teeth grew (Pei et al. 1991). In females, the permanent upper canines did not erupt until 1 year of age, and the size usually did not exceed 5 mm in adults; in males, the teeth could be seen above the gum as early as 3 months of age. However, the lengths of the permanent upper canines were not measurable until the animals were 5 to 6 months of age.

The length, measured in a straight line from the gum-line to the tip of the tooth, grew rapidly until 2 to 3 years of age (Fig. 3).

Table 2. Parametersa of the Logistic model for different growth parameters for the Formosan Reeves' muntjac

	Asymptote	k	to (weeks)	r^2
Eviscerated body weight				
Male	8.50 kg	0.028	21.5	0.942
Female	7.00 kg	0.028	12.8	0.859
Mandibular diastema length				
	37.50 mm	0.064	−4.3	0.977
Male's upper canine length				
	21.50 mm	0.061	57.2	0.863

[a]See text for the details of the definitions for the parameters of growth model.

DISCUSSION

General

Ungulates are generally considered to be precocial (Case 1978a, Bennett and Harvey 1985). Some characteristics of precocial species may be summarized as follows: small litter sizes, relatively long gestation periods, and a relatively large size and a higher level of maturity at birth (Ricklefs 1967 1973, Martin 1981 1984, Bennett and Harvey 1985, Martin and MacLarnon 1985). Having precocial young apparently limits the overall post partum parental investment required for the offspring (Case 1978b).

In the Formosan Reeves' muntjac, final body weights are reached at 2 and 2 to 3 years of age for females and males, respectively; this is a long growing period for a cervid of this size. For comparison, the moose (*Alces alces*), which is 30 times heavier than the muntjac, reaches adult size at a similar age (Verme 1970). The relatively long growing period, which indicates a slow post-natal growth rate, suggests that female muntjacs invest much less than most other cervids on their newborns during the post-natal stages.

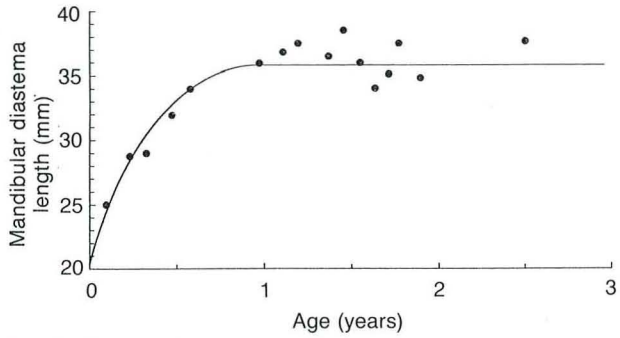

Fig. 2. Best-fitted Logistic growth curve for mean mandibular diastema length for the Formosan Reeves' muntjac *Muntiacus reevesi micrurus*.

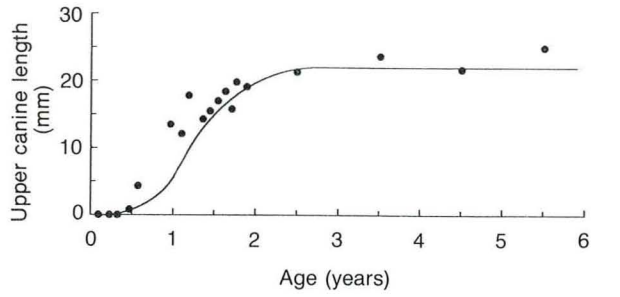

Fig. 3. Best-fitted Logistic growth curve for mean male's upper canine length for the Formosan Reeves' muntjac *Muntiacus reevesi micrurus*.

The energy savings from the lower level of post-natal parental care should be significant for a species like the muntjac in which fawns hide; traveling through the dense understory to the hiding place periodically to feed the young can be very energy consuming for the adult. At the same time, because muntjacs experience post-partum estrus (Soper 1969, Dansie 1970), the low intensity post-natal care required by the precocial young may result in a better post-partum condition for mothers, which favors early post-partum breeding. This would, seemingly, result in an increase in productivity.

Interestingly, since male muntjacs use their tusk-like upper canines as their major offensive weapon (Hoogerwerf 1970, Barrette 1977, Dansie 1983, Morrison 1986, K. Pei pers. obs.), they frequently break or damage these teeth (Dansie 1970). Woodvine (1984) described a canine tooth he found on the body of a 3-year-old male which led him to suspect that male muntjacs may have evolved the ability to replace the canine teeth periodically in order to maintain the usefulness of this important weapon.

The youngest animals with broken upper canines in the present study were 23 to 24 months old and more than 1/4 (12 of 45) of the individuals older than 24 months showed damage to their upper canine teeth. Damage, when present, usually had occurred on both sides, and the degree varied among individuals. In the case of a 23 to 24-month-old specimen, only a small portion of the sharp point of the right canine was lost while the left one remained intact; in another specimen, both canines were broken at the gumline in a 3-year-old animal. However, no sign of regrowth of the canine teeth, as described by Woodvine (1984), was found.

Sexual differences

The results of the present study show that adult body weight exhibits sexual dimorphism in the Formosan Reeves' Muntjac. However, the lack of parallel differences in skull measurements (Wang 1989, this study), suggests that dimorphism occurs only as a difference in body mass but not body dimension (skeleton).

A similar phenomenon has been reported in the spotted hyena *Crocuta crocuta*, in which the female is heavier but not larger in skeletal size than the male (van Jaarsveld et al. 1988). The difference in body weight in the spotted hyena

was suggested as a reflection of the dominance of females over males in food competition (Hamilton et al. 1986). The higher body weight in male muntjacs, therefore, probably indicates the dominant status of males over females, rather than being a result of sexual selection. That may be the case in true size-dimorphic mammals; for example, red deer *Cervus elaphus* (Clutton-Brock et al. 1979 1982), reindeer or caribou *Rangifer tarandus* (Espmark 1964, Bergerud 1974), cattle (Schein and Fohrman 1955), and elephant seals *Mirounga angustirostris* (Le Boeuf and Reiter 1988).

Comments on the equations

Although all equations presented in this paper had high r^2 values, these equations can not be used to estimate the age of young animals for 2 main reasons. First, these equations were calculated on the basis of the mean values of growth parameters for each age-group, yet considerable variations actually existed within each age-group (Table 1). Also, despite the short period that specimens were collected for this study, specimens included females at all stages of the reproductive cycle. Physiological studies have shown that pregnancy and lactation can be very costly in terms of energy and nutrition (Silver et al. 1969, Ullrey et al. 1969 1970, Moen 1973, Robbins and Moen 1975, Robbins 1983). Therefore, difference in reproductive status could produce variations in body weights between female individuals of the same age.

Second, because data were collected from animals belonging to different cohorts, the parameters in the growth curve equation presented here may not be representative of all individuals. Studies on other deer species have shown that a high juvenile growth rate is associated with good habitat quality (Wood et al. 1962, Bandy 1965, McEwan 1968, Klein 1970, Loudon and Milne 1985, Loudon 1987). For animals like the muntjac, in which births occur throughout the year (Pei et al. 1995), young will experience different nutritional conditions during growth. Growth rates, therefore, are expected to vary among different cohorts.

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臺灣山羌(*Muntiacus reevesi micrurus*)出生後之成長模式

裴 家 騏[1]

由1988年12月到1989年1月間，在宜蘭縣共檢視了383隻的臺灣山羌(*Muntiacus reevesi micrurus*)。所有樣本均以其牙齒的生長及磨損狀況做爲年齡估計的依據。結果顯示，下顎牙齒間隙隨年齡的成長沒有雌雄間的差異，且在1歲之後就不再增長。雌性體重的成長在2歲之後即停止，而雄性則持續到3歲左右才停止體重的成長。成年(>2歲)個體中，雄性的體重(平均=8.3 kg)明顯的較雌性(平均=6.8 kg)要重，而這種體重的差異可能反映雄性山羌的社會地位較高於雌性山羌。雄性上顎犬齒的長度在2−3歲以前會持續增加，但成年個體常會發現有犬齒斷裂的現象。

關鍵詞：體重，鹿科，犬齒，成長曲線，性別雙型性。

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