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Age determination in the weasel (Mustela nivalis) in relation to the development of the skull

By CAROLYN M. KING

Animal Ecology Research Group, Department of Zoology, Oxford

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Abstract

Methods of age determination applicable to the weasel are reviewed. The large variability of British weasels in body size and age at reproductive maturity makes classification difficult. The only possible objective criterion is chronological age, even though classes so defined are rather heterogenous. From study of 44 skulls of known age a preliminary method of classification was evolved, which assumes that all weasels are born on 1 June, and then groups them first by month killed and then into first or second year-classes on a combination of characters, principally the closure of the post-orbital constriction. Older weasels, of unknown age, can be separated from the second year-class if necessary by wear of the carnassial teeth. Results given by this method (referred to as the date-skull-baculum (DSB) method, from the 3 essential data) are compared with those given by the periosteal zonation of the mandible, wear of the canines, closure of the sutures, and development of the lateral suprasesamoid tubercle. The best method to use depends on the size and season of collection of the sample: for large samples from one area, especially if collected only in summer and autumn, the DSB method is satisfactory: for small or heterogenous samples, the suture method is best. Periosteal lines in the mandible were clearly visible but related more to the size of a weasel than to its age.

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1 Introduction

There is at present no satisfactory method for determining the ages of weasels. Various authors have attempted to divide samples of weasels into age groups, but none except LOCKIE (1966) was able to relate the characters they observed to known age. For reasons that this paper seeks to show, the lack of known-aged material makes age determination in *Mustela* spp. impossible.

LOCKIE (1966) livetrapped weasels in two areas in Scotland and observed the wearing down of the upper canine teeth in individuals recaptured over periods of up to three years. From these data he calculated the rate of wear and designated six annual age classes, but he has not so far published the details.

Other authors have examined the variation of age-dependent characters in samples of dead weasels of unknown ages. Criteria such as weight of the baculum, development of the sagittal crest, closure of the nasal sutures, and wear of the teeth may all be used to rank individuals in order of age, and then into relative age-groups, but the resulting age structures cannot be compared with each other, and represent unknown chronological intervals (HANSSON 1968; BARBU 1968; FOG 1969; STUBBE 1969).

This technical deficiency has seriously hindered studies of weasel populations, which is regrettable, since the weasel is a common small carnivore in many terrestrial communities, and it would be useful if we could make at least a first estimate of its significance in community interactions, including those on game estates. There are also many other fascinating theoretical ideas, e.g. on the evolution of life history strategies, to which a study of weasels could contribute relevant data from large samples more easily than studies of most carnivores, but not until we can measure age structure and age-specific fecundity and mortality in wild populations (STEARNS 1977).

2 Literature review

General reviews on age determination in mammals have been published recently by MORRIS (1972), SPINAGE (1973), STEENKAMP (1975) and PUCEK and LOWE (1975), so the review below is confined to methods which have been or could be applied to small mustelids.

Throughout this paper the common name "weasel" refers to *Mustela nivalis*, and "stoat" to *M. erminea*. Other *Mustela* spp. are referred to by their specific names.

2.1 Baculum weight and morphology

Age-related changes in the baculum were observed by HENSEL (1881) and other early anatomists, e.g. POHL (1909), CHAINE (1925) and DIDIER (1947): most later workers have used this feature for distinguishing young from adult mustelids, e.g., HILL (1939), POPOV (1943), ELDER (1951), LECHLEITNER (1954), FOG (1969), FITZGERALD (unpubl.), WALTON (1968), VAN SOEST and VAN BREE (1970), and WALKER (1972). WRIGHT (1950) proved experimentally that the development of the baculum is related to secretion of androgens, and is prevented in *M. frenata* castrated before puberty. HEIDT (1970) described the development of the bacula of 10 known-aged *M. rixosa*. Frequency distributions of baculum weight, together with examination of morphology, are sufficient in *M. vison* to distinguish young from adults (GREER 1957).

2.2 Development of the skull, particularly of the post-orbital constriction

HENSEL (1881) gave an accurate description of the narrowing of the post-orbital constriction in stoats and showed that skulls could be arranged in a row of age-ranks on the basis of this feature, and others such as the closing of the sutures. MAL'DZHYUNATE (1957), BOISE (1975), and BUCHALCZYK and RUPRECHT (1977) used it to define age classes in marten (*Martes martes*), fisher (*Martes pennanti*) and polecats (*Mustela putorius*) respectively. Other writers have observed it but for various reasons not used it (LECHLEITNER 1954; HAMILTON 1933; VAN SOEST and VAN BREE 1970).

Other cranial indicators of increasing age include the closing of the nasal sutures (Hall 1951; Hansson 1968), the relationship between the widening zygomatic breadth and the narrowing post-orbital breadth (Anderson 1970), sagittal crest (Hill 1939; Reinwaldt 1959; Fog 1969; vanSoest and van Bree 1970), and the general shape and texture of the cranium (Hall 1951; Fitzgerald unpubl.). Vershinin (1972) found that a comparison of characters reflecting the shape of the skull "distinguished with sufficient clarity the skulls of first-year from older stoats".

Most cranial features give good separation of juveniles, but the rate of change slows down later. The definition of classes in a smooth growth series is often arbitrary and difficult, but the post-orbital constriction continues to develop for longer than any of the other features (van Bree et al. 1966) and can be measured, though of course the classes so defined show considerable overlap.

2.3 Dentition

Small mustelids develop adult dentition early (Hamilton 1933; Hill 1939; Mazak 1963) and few with milk teeth appear in collections. Stroganov (1937) constructed a key recognising 6 year-classes based on wear of the carnassial teeth in stoats, but Hill (1939), Lechleitner (1954) and van Soest and van Bree (1970) concluded that toothwear in their material was too variable to be of use in age determination.

2.4 Lateral suprasesamoid tubercle (LSST)

This small bony process on the distal end of the femur is claimed to offer a reliable means of separating juvenile from adult stoats (van Soest and van Bree 1970), mink, *M. vison* (Lechleitner 1954; Greer 1957), and *Martes* spp. (Leach et al. in press). It is particularly valuable in females, which lack a baculum. It has not been tried in weasels.

2.5 Growth lines in bones and teeth

This method, unlike any of the above, is based on discontinuous growth. The presence of growth-lines is well documented in many species (Klebanova and Klevezal' 1966; Klevezal' and Kleinenberg 1967, and many recent specific descriptions) and their correlation with an annual cycle of growth is usually assumed (Sergeant 1967). Klebanova and Klevezal' (1966) state that stoats have a maximum of 3 periosteal lines, and that weasels have none. Van Soest and van Bree (1970) found a good correlation between canine cementum lines and baculum weight in 37 stoats. If reliable, growth lines could be more accurate than any other method of age determination; if not, more misleading.

2.6 Other methods

Some known methods were not tried in this study. The time of closure of the femoral epiphyses is a function of size and sex, rather than age, in *Martes* spp. (Dagg et al. 1975). In stoats and weasels they close too early to be useful. The weight and chemistry of the eyelens (Pelton 1970; Otero and Dapson 1972) are greatly affected by temperature and the state of preservation of the carcasses. Most of my material was stored deep-frozen, and some was not very fresh when collected. Body weight, used to indicate age by Fog (1969), may vary in live individuals from day to day by up to 13% of the mean for 4 days (King 1975), as well as with season and area, and is clearly not a suitable criterion for age determination.

3 Material and methods

3.1 The problem of defining age classes

There are two possible approaches to the problem of determining age in cases where known-aged material is insufficient or absent. One approach is to arrange the specimens into natural age classes, bounded by definable characters regardless of what chronological intervals they represent. Most studies using continuously developing characters, such as the skull and baculum, use this method, though because these characters form a growth series, the measurable features overlap between classes, and the non-measurable ones are difficult to judge. Statistical tests applied to such data often reject characters which could be used if some way of overcoming the problem of overlap could be devised. The second approach is to decide the chronological interval required beforehand, and then examine the specimens to see if they can be reliably placed in these classes. This method is essential in all studies dealing with discontinuous criteria, such as annual growth lines in bones and teeth, and also when the sample is to be divided into year-classes, by whatever method, for population analysis. It is the more flexible of the two approaches, because if the first-year group is distinguished from the rest, it can often be subdivided into natural groups if desired; but natural groups defined without reference to the date of death cannot be rearranged to give year-classes.

3.2 Characteristics of weasels causing difficulties for age determination

3.2.1 Reproduction

Females are fertilised in spring, implant immediately and produce young in about 35 days. Lactation lasts about 3–5 weeks and families break up by 9–12 weeks (Corbet and Southern 1977). In seasons of abundant food, adult females may produce a second litter in summer, and some of the early-born young females may breed in the season of their birth. Early-born young males may also be well developed by the autumn, when in males of all ages the gonads regress and ossification of the baculum ceases. Hence, the overwintered young animals of either sex approaching the next breeding season may be from 5–10 months old, and their gonads and bacula may be either completely immature or in any stage of transition to the adult form. This variability makes the cohort of young very heterogenous and soon overlapping with the adult class. Hill (1939) graphically described the difficulty of classifying weasel skulls without known-aged material, and Stubbe (1969) concluded that the only way to determine the ages of weasels is by comparison with known-aged skulls.

3.2.2 Variability in body size

Sexual dimorphism is pronounced and males vary greatly both within and between populations. The range of mean body weights of males in 5 British samples was 107–131 g, and of condylobasal lengths, 37.0–40.1 in 7 samples, tending towards larger males in the north of Britain (King 1977). In one area observed the mean weight of resident males was 115 g in one winter season and 100 g in the next (King 1975). Females vary less, individually and geographically, and reach their adult body size slightly earlier than males (Corbet and Southern 1977). Late born young of either sex may not be fully grown by winter and remain small until spring (Hill 1939). Most skeletal characters develop to different degrees in individuals of the same age but different sizes (Wright 1947; van Soest and van Bree 1970). Those intended to be correlated with age must be used with caution.

3.3 Definitions of age classes in weasels

Clearly, the biology of weasels makes the definition of natural age groups difficult. Criteria of reproductive maturity or body size separate the immature from the mature at different ages, according to when in the season they were born. The only useful objective definition is based on chronological age, irrespective of physical or reproductive maturity. Hence, this study uses the second approach to age classification. First I examined a series of known-aged skulls for means of distinguishing year-classes. Then I used a sample of wild-caught weasels to compare the results given by the known-aged criteria and by several methods described by previous authors. The finalised method was proven in practice on several further collections (not discussed here) before being considered for publication.

Weasels caught before June of the season after their birth are called "Young", a non-committal term not implying anything about their reproductive status. Second-year weasels are certainly all adults so it is safe to label this class "Adult". Weasels older than 2 years are called simply "Old". The term "first-year" for the first group has been avoided because young weasels may in fact be any age up to 14 months old. Likewise, weasels in the second year-class may be from 10 to 26 months old. The upper age limit of the third group is not known.

3.4 Material

3.4.1 Known-aged skulls

Dr. Fritz Frank of Braunschweig (W. Germany) kept a colony of weasels for about ten years, in which 94 young were born. He kept the carcasses of 44 (26♂♂, 18♀♀) which died naturally or accidentally, together with the dates of birth and death, and records of body length and weight, breeding condition and history. He cleaned the skulls by boiling, and kept the carcasses in preservative. He kindly allowed me to examine the skulls and records, and to extract and clean 16 bacula from the carcasses. I did not extract the femurs. Of the 44 weasels, 70% were less than one year old, an age distribution similar to that of wild weasels. Each skull was photographed and measured (Fig. 1).

3.4.2 *Wild-caught weasels*

Carcasses of 171 weasels were collected from gamekeepers on 3 game estates in Sussex, Northumberland and Wigtownshire, and from Wytham, a reserve in Berkshire where a livetrapping study was in progress (KING 1975). Most were killed in the humane "Fenn" spring trap, which kills almost instantly and allows the collection of specimens with teeth undamaged by attempts to escape (KING and EDGAR 1977). Carcasses were preserved frozen and cleaned by dermestid beetles. The same material was included in a previous paper, where full details of the collections are given (KING 1977: sample nos. 4, 5 and 6 plus the first 55 of sample 1).

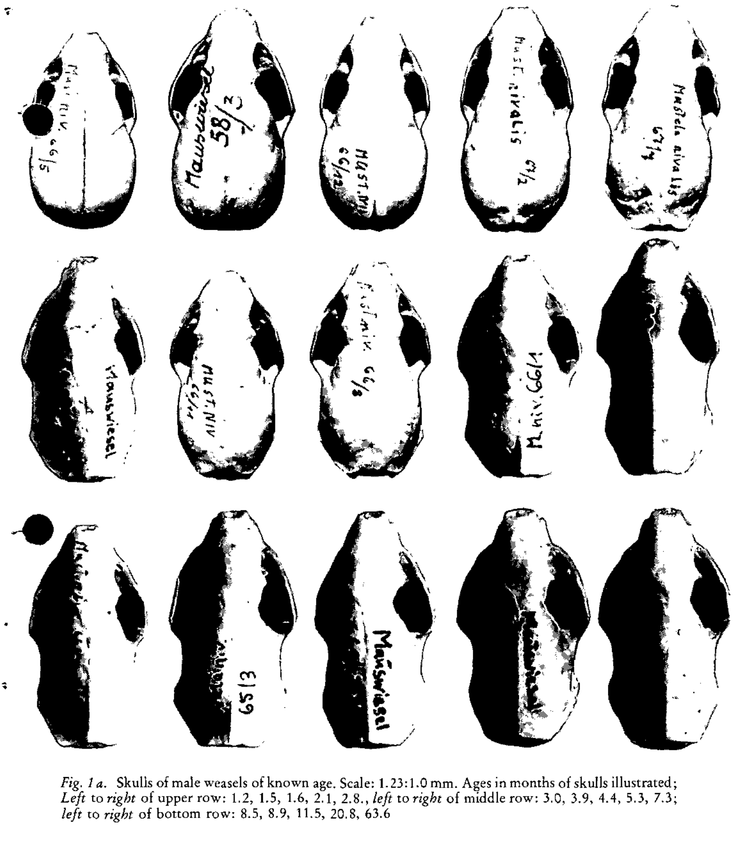

Fig. 1 a. Skulls of male weasels of known age. Scale: 1.23:1.0 mm. Ages in months of skulls illustrated; *Left* to *right* of upper row: 1.2, 1.5, 1.6, 2.1, 2.8., *left* to *right* of middle row: 3.0, 3.9, 4.4, 5.3, 7.3; *left* to *right* of bottom row: 8.5, 8.9, 11.5, 20.8, 63.6

3.5 Laboratory procedures

Clean skulls were measured with a vernier micrometer (Fig. 2). Bacula were air-dried, measured and weighed to the nearest 0.1 mg. The development of the lateral suprasesamoid tubercle of the femur was estimated by eye on a 3-point scale from the photographs given by van Soest and van Bree (1970). The state of closure of the nasal sutures was estimated by eye on a 4-point scale after Hansson (1968). The degree of wear on the canine teeth was estimated by eye on a 6-point scale from photographs of the skulls

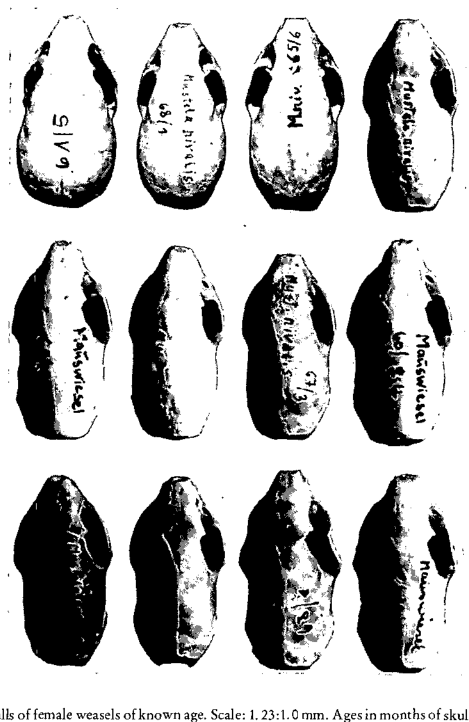

Fig. 1 b. Skulls of female weasels of known age. Scale: 1.23:1.0 mm. Ages in months of skulls illustrated: *Left* to *right* of upper row: 1.5, 2.9, 3.3, 6.3; *Left* to *right* of middle row: 11.1, 12.0, 16.8; *Left* to right of bottom row: 17.3, 19.4, 31.1, 38.5

of known-aged wild weasels kindly loaned by Dr. J. D. LOCKIE. One mandible from each skull of the weasels from the game estates was decalcified whole for 7 days in 5% trichloroacetic acid. Transverse sections were cut at about 35 μ on a freezing microtome through the mandible and the anterior cusp of the lower carnassial tooth (M_1) together, stained with Mayers haemalum and mounted in Canada Balsam. Mandibles of weasels from Wytham were not sectioned, except those from animals with a known history.

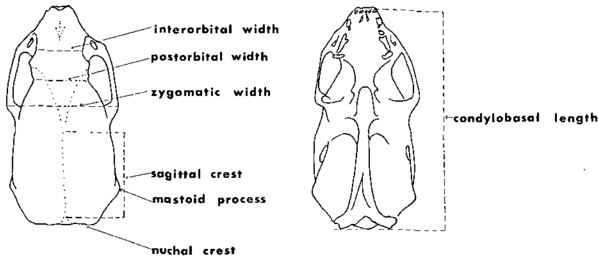

Fig. 2. Cranial nomenclature

4 Results

4.1 Characters related to age in known-aged weasels

Representative stages in the development of the known-aged skulls are illustrated in Figs. 1a and b. In most respects the skull of the weasel reaches adult form by the age of 6 months. The nasal sutures in both sexes are coalesced by 3 months, and invisible after 6 months. In females the sagittal crest is more variable than in males and may not reach fully adult form for 12 months. Only the post-orbital constriction changed over a long enough period in both sexes to distinguish year-classes, and was easy enough to observe to be of practical value. In young of both sexes under about 3 months old the post-orbital width is greater than the inter-orbital width. In males the post-orbital width narrows to equal the inter-orbital at 4–6 months, and thereafter continues to narrow slowly, probably throughout life. In few females does the post-orbital width become much less than the inter-orbital, and then not until after 12 months of age. The regressions of the ratio of post-orbital to interorbital width, called here the post-orbital ratio, on months of known age are $r = 0.89$ for males, and $r = 0.78$ for females, both significant at $P < 0.001$ (Fig. 3). These data confirm the statement of PETROV (1956), that the skull of the female mustelid is not a reduced copy of the male: it has a different growth rate and retains more juvenile features in the adult than does the male. This needs to be borne in mind when comparing the growth series of male and female skulls.

Both weight and length of the baculum increase significantly with age (Fig. 4). The variance ratio is not significant, probably because of the small sample size, but suggests that weight is the better correlate. Females have no baculum, but though this is compensated for to some extent by the longer time over which post-orbital narrowing proceeds, age determination is still less reliable in females.

Although the captive young were born at various times of the year their skulls have been arranged as a single growth series for the purpose of comparing with skulls of unknown age. If season of birth had any effect on their growth rate, it is scarcely detectable (Fig. 1). But weasels born in the wild may not be so consistent, and this too is a factor that should be borne in mind when using Fig. 1 as a standard.

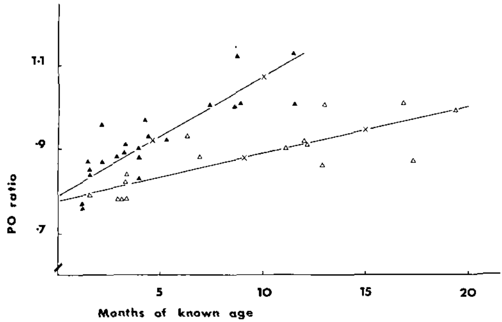

Fig. 3. Regression equations for post-orbital ratio against known age in male and female weasels. Closed symbols = males. X = calculated regression points. Males: $y = 0.800 + 0.028\,x$; $r = 0.89$, $P < 0.001$. Females: $y = 0.783 + 0.011\,x$; $r = 0.78$, $P < 0.001$

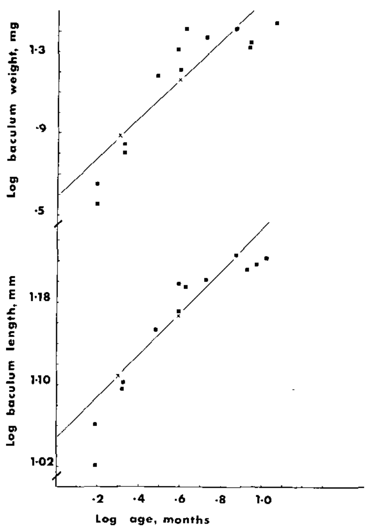

Fig. 4. Development of the baculum in weasels of known age.
Above, weight: $y = 0.614 + 0.915\,x$; $r = 0.85$, $P < 0.001$
Below, lenght: $y = 1.050 + 0.197\,x$; $r = 0.83$, $P < 0.001$
Variance ratio $F = 1.108$, $P \nless 0.05$

The captive weasels were fed only on live *Microtus* from an adjacent laboratory colony. The carnassial teeth of the known-aged skulls showed no exposure of dentine until past 2 years of age. This criterion, though less reliable than the others, can be used if necessary to give an approximate upper limit to the second year-class. For some analyses it could be useful to remove weasels in their third year or older, whose actual age is unknown.

4.2 A comparison of methods for age determination in weasels

In this section, the results of applying various methods of age determination to the sample of 171 wild-caught weasels are compared. The first method is derived from my study of the known-aged material described above; the others include as many as practicable of the previously known methods summarised in the review.

4.2.1 The date-skull-baculum method (DSB)

The basis of this method in practice is classification by year class and date, not by absolute age. The skulls are laid out, each sex and sample separately, in 12 groups according to the month of death, beginning in June. In each month-group the young of the previous season are separated from the older weasels, giving 2 series of 12 groups each. When correctly arranged the 2 series form a continuum showing the development of the cranium and baculum. A skull collected in a known month could fall into one of only 2 groups, and, because of the year's difference in growth between them, was conspicuous if misplaced in the first 6 months of the series, though less so later. Criteria of shape (including the appearance of the post-orbital constriction, the sagittal and nuchal crests and the mastoid processes) and texture of the bone were important. In males, the weight and conformation of the baculum was also taken into account, and all doubtful cases checked against the photographs of the known-aged skulls (Fig. 1).

Because of the geographical variation in size of British weasels, age classification based on this ranking method should be done strictly within localities. Further, the whole sample from one place should be examined simultaneously, because the process is comparative and classification of single specimens is hazardous. If the date of death is not known, classification should not be attempted, except in the case of obvious juveniles under about 3–4 months old.

The median birth date of British weasels was taken as 1 June, from the monthly distribution of pregnant and lactating weasels found in these collections and by Deanesly (1944). The season of births is long, about 4–5 months, so "age" counted from 1 June is the mean of a range of ages of perhaps 2 months each way. The first few monthly groups of the first year class will contain skulls which are obviously either early-born or late-born, and, from comparison with the known-aged skulls, different in absolute age by up to 2 or 3 months; later, the distinction blurs. There may even be a few very young animals caught in May, which have to be added to the June group of young. The only objective way to deal with this situation is to make the classification by year class and date, not by age, even though this means that the members of a particular monthly group may span a range of ages according to their birth date. In some continental countries, and in North America, there appears to be no definite breeding season at all (Pohl 1910; Hall 1951); this method is not applicable there.

The skulls of most British weasels are damaged in the post-orbital region by *Skrjabingylus nasicola*, a destructive nematode parasite (King 1977). In samples from districts where *S. nasicola* is common, the post-orbital widths cannot usually be measured and plotted for all skulls, as in the known-aged weasels. However, this is not too serious, as the difference in post-orbital ratio between two weasels a year apart in age was usually clear despite the damage (Fig. 5), so almost all skulls could still be assigned to a year class (Table 1).

The sagittal crest, an obvious feature used for age determination ever since it was de-

Table 1

Percentage year-class ratios given by three independent methods for 4 samples of weasels

	Date-skull-baculum	Mandibular periosteal lines	Canine wear
Sussex			
0–1 year	85.5	O 52.3 } R 38.6 } 90.9	63.6
1–2 years	14.5	9.1	29.0
2–2 years }	0		5.6
3–4 years }			1.8
n	55	44	55
Northumberland			
0–1 year	66.7	O 23.9 } R 16.3 } 40.2	37.0
1–2 years	31.5	32.4	59.3
2–3 years }	1.9	13.5	3.7
3–4 years }		13.5	0
n	54	37	54
Wigtownshire			
0–1 year	78.9	O 14.3 } R 14.3 } 28.6	17.7
1–2 years	21.2	21.4	52.9
2–3 years }	0	35.7	23.5
3–4 years }		14.3	5.9
n	33	28	34
Wytham			
0–1 year	67.9	Sample	37.1
1–2 years	28.6	too	29.6
2–3 years }	3.5	small	22.2
3–4 years }			11.1
n	28		27
Total sample			
0–1 year	74.9	57.8	41.8
1–2 years	24.0	20.2	43.5
2–3 years	1.2	13.8	11.2
3–4 years	0	8.3	3.5
n	171	109	170

scribed by H*ENSEL* *(1881), is helpful in distinguishing year-classes. Its development* greatly influences the shape and maturity of the skull, and, unlike shape, it can be measured. But the length of the sagittal crest cannot be used as an objective criterion of age. The rate and extent of the development of the crests of the skull are related to the size and work of the jaw muscles inserted into them (BELL 1956); body size may influence their appearance more than sex or age. In 41 male weasels of the same age from 3 areas of Britain, collected between January and March of their first year, the mean length of the sagittal crest varied as follows: Sussex, 17.5 mm (n = 10); Northumberland, 18.9 mm (n = 14); Wigtownshire, 20.9 mm (n = 17). The mean body weights of males from these areas were 109 ± 0.9 g, 121 ± 4.3 g and 131 ± 3.1 g respectively. Hence, age structures based on this criterion could be misleading; this is the main reason why the DSB method of age determination in the geographically variable British weasels can be done only within local samples, not on heterogenous collections or on individuals.

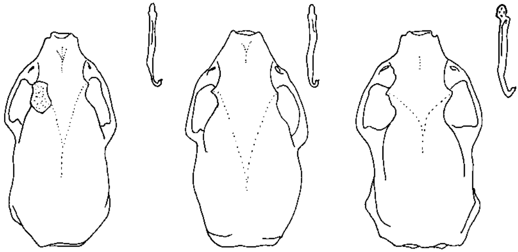

Fig. 5. Determining the age of a weasel in practice. *Left:* The skull and baculum of a wild weasel of unknown age killed on 17 Sept. 1969. Taking the median birth date as 1 June, this weasel could be either about $3^1/_2$ months old or about $15^1/_2$ or more months old. Compare with the skulls and bacula of weasels of 3.3 (*center*) and 11.5 (*right*) months of known age. Despite the distortion of the post-orbital constriction caused by *Skrjabingylus* it is still possible to say with certainty that the left hand specimen was a young weasel.

4.2.2 Periosteal zonation

Growth lines in the periosteal zone of the jaw sections were clearly visible, but difficult to interpret. Some lines were shorter than others, or very close together: do "half" and "double" lines still count as one? (Fig. 6). The "resorption line" of KLEVEZAL' and KLEINENBERG (1967) was usually, though not always, visible and was recorded as "R". Its significance in the weasel is unknown. Six weasels of known history from my live-trapping area (KING 1975) were not helpful in interpreting lines, and one caught as a juvenile and kept in captivity for 18 months showed no lines (Table 2). Even though I followed the instructions of KLEVEZAL' and KLEINENBERG (1967) on interpretation, 26% of all sections had to be rejected because they could not be read. Age distributions, calculated assuming one line equals one year, are shown in Table 1.

Table 2

Periosteal layering in mandibles of weasels with a known history, from Wytham Wood (King 1975)

Tag No. and sex	Months between first and last capture	DSB age	Growth lines visible	Date of death
♂ 13	4	Young	R + $^1/_2$	12. 3.69
♂ 10	5	Young	O	13. 3.69
♂ 7	6	Young	O	10. 3.69
♂ 8	8	Adult	O, ? 1 forming	12. 5.69
♂ 11	12	Adult	R + $^1/_2$	30.10.69
♂ 22	12	Adult	R + 1 forming ? (Fig. 6)	9. 6.70
♀ Captivity	18	Adult	O	10.12.69

Ages at first capture were unknown, except that ♂ 22 was probably born on the study area in June 1969, and the captive female was caught on 3.7.68 aged <50 days (milkteeth present, see MAZAK 1963).

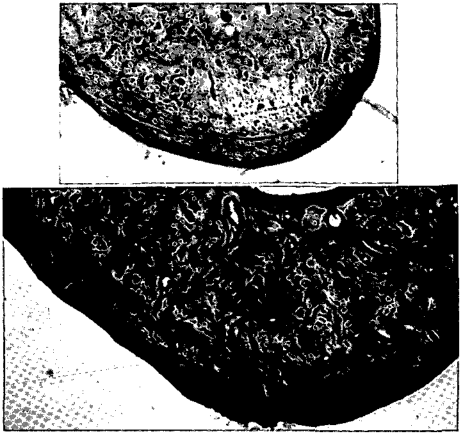

Fig. 6. Difficulties in counting periosteal layering in the mandibles of weasels. *Above:* ♂ 22 from Wytham, known to be 12 months old (table 2). *Below:* A male from Northumberland killed in August of its second year (c. 14 months old) Both × 54

4.2.3 Wear of the canine teeth

The main attraction of this method is that one might use it on living animals. I applied it throughout a live-trapping study of 22 months (KING 1975) and found a wide individual variation in rate of wear. The time over which I was able to recapture live individuals ranged from 6 weeks to 12 months, and the overall rate of wear appeared to be about twice that estimated by LOCKIE from Scottish material. Two of LOCKIE's categories were passed in one year or less (16 weasels observed).

I also applied the method to the 171 skulls and found difficulty in being consistent in assigning specimens to the 6 age categories, and also in recognising teeth which had been broken and subsequently levelled by wear. Age structures are shown in Table 1.

4.2.4 The baculum used alone

Both weight and length of the baculum are related to age (Weight, $r = 0.69$, $P < 0.001$; Length, $r = 0.46$, $P < 0.001$), but the variance ratio of $F = 1.514$ shows that weight (Fig. 7) is significantly better correlated than is length ($0.05 > P > 0.01$). The distribution of baculum weights for all the 121 males together is almost a normal curve (Fig. 8); the slight trace of bimodality offers little prospect of using baculum weight unaided to divide age groups without massive overlap. Conformation is not helpful either, because bacula can be arranged in a series showing a smooth transition from the simple juvenile form to the fully developed proximal head of the adults.

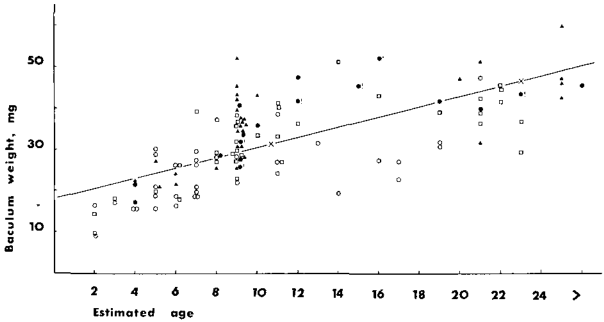

Fig. 7. Weight of the baculum plotted against estimated age in months (DSB classes: July of the first year = 1 month old, etc.) in 121 wild-caught weasels. Symbols: ○ = Sussex; □ = Northumberland; ● = Wytham (! tagged individuals); ▲ Wigtownshire; x = calculated regression points. $y = 18.5 + 1.23x$; $r = 0.69$, $P < 0.001$

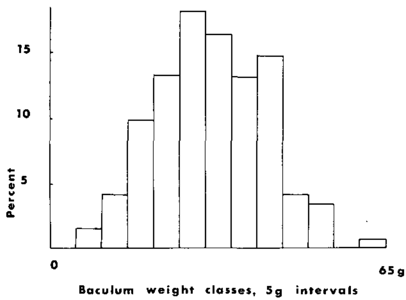

Fig. 8. Frequency distribution of baculum weights of 121 male weasels of unknown age

4.2.5 Nasal sutures

The four age-groups defined by HANSSON (1968) from the state of suture closure are relative only, and hitherto there has been no information from which to estimate the range of ages they represent. For weasels (but not larger species of *Mustela,* in which suture closure takes longer) approximate calibration is now possible (Table 3). This makes the suture closure method much more useful, especially for small, heterogenous or undated samples for which the DSB method is inappropriate. The results agree reasonably well. My sample contained 21% weasels killed before 31 December of their first year, which could be up to 8 months old. The suture closure method designated 25% of the sample as belonging to Classes I–III, up to 6 months old.

The main disadvantage of using this method alone for weasels is that sutures close early in small animals, so there are 3 categories for weasels aged up to 6 months, but only one for all older ones. This means that the relative proportion of the 4 classes is greatly influenced by the season of collection. For example, most of my 171 weasels were collected in spring, so there were only 8% young in Classes I and II (under 3 months old) while overwintered young and adults fell together into a large group (75% of the sample) in Class IV. By contrast, HANSSON's (1970) sample, presumably including many weasels caught in summer, contained 40% young less than 3 months old. Yet the year-class distribution of the two samples could well be the same. If the suture method is used alone to determine age distributions for population analysis, season of sampling must be controlled, and this is not always possible. For large samples it is better to use suture closure only to help distinguish year classes by the DSB method.

Table 3

Distribution of categories of suture closure

		% skulls per category I	II	III	IV
HANSSON's categories		Open	Coalescing	Coalesced but visible	Invisible
Age at this stage in *known-aged material*		*<3 Months*		*3–6 Months*	*Over 6 Months*
Sample	n				
Present work	167	0.6	7.8	16.7	74.9
HANSSON (1970)	319	21.6	17.9	19.7	40.8

4.2.6 Lateral suprasesamoid tubercle (LSST)

As in the larger mustelids, the development of this tubercle was related to age. It was not present or developing on any small young caught up to September, and it was not completely absent on any adults. But after October, some young already had a fully developed tubercle, and on some adults it was still incompletely developed. In the intermediate group, young caught between February and May, all stages of development were found (Table 4).

Table 4

State of the lateral suprasesamoid tubercle (LSST)

LSST	Numbers per DSB class Young June–Sept. ♂	♀	Oct.–Jan. ♂	♀	Feb.–May ♂	♀	Adult ♂	♀	Totals
Present	0	0	6	8	21	4	24	8	71
Developing	0	0	16	3	23	11	8	2	63
Absent	6	1	4	1	2	2	0	0	16
Totals	6	1	26	12	46	17	32	10	150

This feature is most useful in the negative: absence of the tubercle always identifies a young weasel, but its presence does not necessarily identify an adult. Like nasal sutures, it can be a useful aid to distinguishing year-classes by the DSB method, but is insufficient alone except for samples collected only in mid or late summer. If a summer sample is planned, skulls need not be cleaned, which saves a great deal of work; if skulls are collected but broken in preparation (particularly likely to happen to young specimens), the LSST reliably distinguishes young from adults until September.

5 Discussion

5.1 Comparing the methods tried

Three of the methods tried gave independent estimates of the yearclass ratio of the sample (DSB, periosteal lines, canine wear); one a relative classification up to 6 months (sutures); and 2 others were rejected for use alone (baculum and lateral suprasesamoid tubercle), though both are helpful when incorporated into the DSB procedure. Table 1 compares the results given by the first 3 methods. There is considerable disagreement between them, and none is statistically very rigorous. This is to be expected in view of the great variability of the material.

The only character known from empirical evidence to be related to age is the growth of the baculum (Wright 1950). Hill (1939) gave the maximum weight of the baculum of first-year weasels as 21 mg. The sample contained 26 young males with bacula of 21 mg or less: of these, the periosteal layering and canine wear methods designated 1 and 6 respectively as adults. This check cannot be applied to the DSB method, since the baculum weight is part of its process: however, in one sample of British weasels in which the damage caused by *Skrjabingylus*

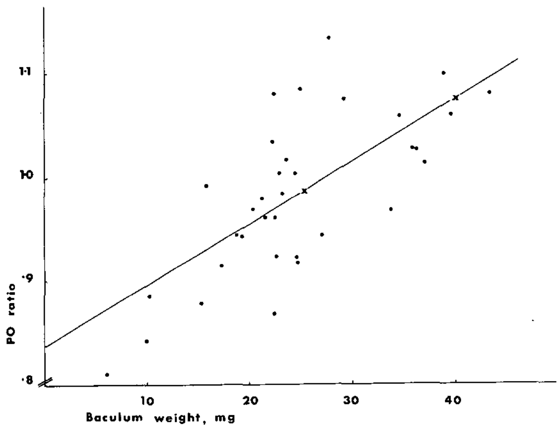

Fig. 9. Post-orbital ratio plotted against baculum weight in weasels in which damage by *Skrjabingylus* was slight or absent (sample comprises 35 of 73 males from South Oxfordshire: see King 1977). x = calcultated regression points. $y = 0.836 + 0.006\,x$; $r = 0.77$, $P < 0.001$

nasicola was relatively slight, the post-orbital ratio could be measured and plotted against baculum weight for 35 males. The correlation was highly significant ($r = 0.77$, $P < 0.001$; Fig. 9).[1]

5.2 Choice of a method

The choice of a method of age determination depends on the kind of material in hand and the purposes of the analysis.

5.2.1 Specimens collected all year round

For various good practical and biological reasons a sample may have to include animals killed at any time of year. If the intended analysis requires distinction of year classes, the DSB method is less unreliable than the periosteal or canine wear methods. Its accuracy is greatest up to 9–10 months, so it is most sensitive for the bulk of the sample; it is a composite method, taking into account several factors and hence can allow for variability between samples not related to age; and it was established by study of material of known age. On the other hand, it is open to criticism on the grounds that it compares wild and captive animals, it is subject to interference by the destructive cranial parasite *Skrjabingylus nasicola,* the classification process is visual and qualitative, its resolution declines with age, and the ages of the oldest animals are unknown.

Not all analyses require distinction of annual cohorts, but if the specimens are already all classified by year-class and date, division of the sample for analysis can be at whichever month in the first year-class is appropriate for the question in hand. For example, for an analysis of geographical variation in body weight in male weasels, the juveniles would be separated out by making the break-point in December of the first yearclass, but if the analysis required every individual to be reproductively mature, only overwintered weasels killed after March of their first year would be used. For a description of the development of, say, damage from parasitism, the first year class can give up to 12 groups plus a single group for adults (King 1977). So long as first-year animals are distinguishable, the sample can be arranged in whatever way gives the best compromise between the needs of the analysis and the decreasing certainty of age classification through the year.

5.2.2 Specimens collected only in summer/autumn

The problem of declining accuracy can be largely overcome if field collections are carefully designed. The DSB method gives accurate results at least to December; it is simple, does not require elaborate laboratory preparation, and is sufficient for many purposes, if field collections are confined to summer and autumn. For example, in theory the best time to take a sample for population analysis is just after the season of births, when the current season's crop of juveniles have been added to the population and the period of presumed winter mortality has not begun. It is also the time when trapping success is high (Jefferies and Pendlebury 1968). The only type of study that could not be served by the DSB method in these circumstances is one that needs to know the maximum longevity of the old weasels.

[1] *Note added in proof.* A recent paper by Jensen, B. (1978): Resultater af fangst med kassefaelder (Natura Jutlandica 20, 129–136), mentions that, from sections of the canines of 48 weasels collected in Denmark, 35 could be classified as 0–1 year old, 8 as 1–2 years old, and 5 as 2–3 years old. This age-distribution agrees remarkably well with that given by the DSB method (Table 1). If Jensen's method can be calibrated against known-aged material from the wild, it could be used by workers who require accurate age-determination of adult weasels. The DSB method would then be most suitable for certain collections made with more simple aims and equipment, or when destruction of material by sectioning is for some reason undesirable.

5.2.3 Heterogenous collections

Because the DSB method can be applied only within large, dated and homogeneous samples, collections which are small or of diverse geographical origin, or in which the date of death of each specimen is unknown, can be classified only by the suture method.

5.3 The problem of variability

All the age determination methods used here are based on the study of bone, a living material sensitive to numerous influences during its formation and constantly changing its substance even in the adult (SIMKISS 1975). The amount of variation found in bone characters should therefore cause no surprise. The pattern of periosteal zonation in weasels is a particularly remarkable example of this sensitivity of bone structure to influences other than age.

Though the DSB method gave similar age structures for the three subsamples of weasels from Sussex, Northumberland and Wigtownshire, the counting of periosteal lines gave 3 different age structures, two of them highly improbable (Table 1). On theoretical grounds, the Wigtownshire population should be in danger of extinction, yet trapping on that estate is carried out all the year round and produces a regular crop of weasels. The most obvious differ-

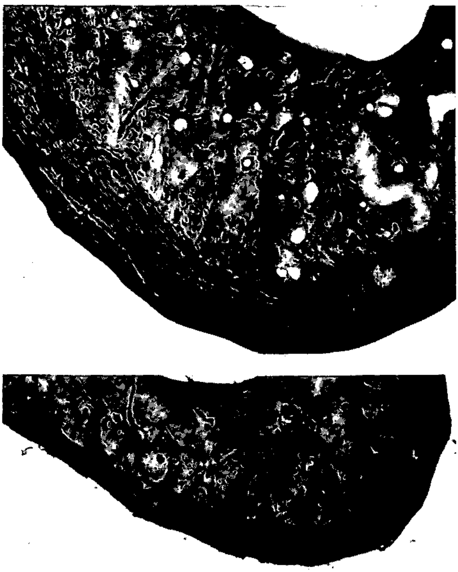

Fig. 10. Influence of body weight on the number of periosteal lines in the mandibles of weasels. *Above:* Male from Wigtownshire, weight 150 g. *Below:* Male from Sussex, weight 116 g. Both animals were estimated by the DSB method to have been killed in March of their second year. (Both × 54)

ence between the samples was in body weight. Regressions of the number of jaw lines against body weight and against DSB age were, as might be expected, both significant (weight, $r = 0.52$, $P < 0.001$, $n = 79$; age, $r = 0.49$, $P < 0.001$, $n = 79$): but $F = 1.10$ ($P > 0.05$), i.e., slightly more of the variation in number of jawlines could be explained in terms of body weight than in terms of DSB age (27.6% as opposed to 23.7%). Fig. 10 shows the jawlines in two weasels, which, according to DSB classification, were both killed in March of their second year. The one from Wigtownshire weighed 150 g and shows at least 4 lines plus a resorption line; the other, from Sussex, weighed 116 g and shows only a resorption line. (However, this explanation does not hold for females, in which there was less geographical variation in body weight and no tendency to associate higher body weights with more northerly sampling areas.) Periosteal lines are also known to be subject to reformation (KLEVEZAL' and KLEINENBERG 1967) and, as pointed out by STEENKAMP (1975), do not necessarily give chronological age, and so should be related as far as possible to other criteria. The example of these weasels confirms these authors' warnings, and emphasises that we should remain cautious in using any kind of growth lines in weasels until they are shown to be annual.

The DSB method minimises the problem of variability by reducing as far as possible the choice of classes into which a specimen may fall. Classification is a two-stage process: first by date (month killed), and secondly by year-class. Since the date is known (if it is not, the method is not applicable) the first stage does not involve any choice: and as only two year-classes are required, the second stage involves a choice between only two possible classes, even though there are 24 classes in all. Variation in a character between adjacent months within the first year-class is often large in a growth series, but it is irrelevant; what is important is the variation in that character between year-classes in a given month of death. If two skulls have a year's difference in growth and development, the difference in shape is usually clear to the eye, when they are compared with each other and with an appropriate known-aged shape from Fig. 1. Though this method gives only two basic year-classes, it is enough for most purposes in the weasel, a short-lived animal in which more than half the specimens are in their first year. However, for population analysis they must be year-classes, because otherwise differences in the date of collection of, say, two samples from the same cohort can greatly affect the age-ratios found (for an example, see Table 3, and also KING 1977). Separation of the old weasels from the adults is an optional third stage.

The reduction of choices does not, however, dispose of the need for known-aged material, so the DSB method cannot be applied to other *Mustela* spp. unaided. It was tried on a large collection of stoats from New Zealand (KING unpubl.) but the young could not be reliably distinguished past 5 months of age, when they no longer formed a distinct group. Classification could still be made past this age, but because of the great variability in the skulls of *Mustela* spp., the lack of known-aged material to refer to made the groupings rapidly more and more arbitrary (as measured by the extent of disagreement between observers). However, for the summer months the method was quite satisfactory.

The problems of age determination in small mustelids were aptly summarised by HALL (1951) "... the skulls of weasels offer fewer features for estimating age than do those of most mammals ... More reliance on shape of entire skull and less reliance on extent and shape of any individual bone is necessary in estimating the age of a weasel". The "shape" of young and adult skulls is easily recognised as different, but "shape" is not easily classified with rigorous consistency. The method described here is a start, but is not ideal, partly because the material is so variable and partly because the method itself is not entirely quantifiable or objective. Rather than despair (which one is frequently tempted to do in age-determination work) I think it is better simply to take one step at a time. If the best available method will give only a first approximation, that is at least better than one which, like periosteal lines, is precise but inaccurate, or else nothing at all. Age determination is a means, not an end in itself.

For example, in taxonomy, it is valuable to be able to distinguish and discard the skulls of young animals when listing the characteristics of a species. The taxonomy of weasels has been confused in the past by the use of criteria such as the degree of development of the post--orbital constriction, and sagittal crest, which are greatly affected by age and body size. Several works (reviewed in BEAUCOURNU and GRULICH 1968) assert the existence of a separate, smaller species of weasel in Europe, *Mustela minuta* Pomel, defined in such terms (among others), and descriptions of museum collections are almost never adequately controlled for variation with age. Or, an evironmental manager may have to make a decision, or to make a survey of his area prior to making a decision, which cannot wait indefinitely while a perfect method of age determination is developed. From his point of view it may be enough to have a method which is reasonably correct within its limits, and to know what methods to avoid. More work is needed to find a method equally accurate at all times of year: in the meantime, the DSB method can be used with caution to give a first estimate of the structure of weasel populations (KING 1980).

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Zusammenfassung

Altersbestimmung beim Mauswiesel (Mustela nivalis) in Beziehung zur Schädelentwicklung

Es werden mehrere Methoden zur Altersbestimmung beim Mauswiesel überprüft. Die große Variabilität britischer Mauswiesel in Körpergröße und Alter bei Erreichen der Geschlechtsreife erschwert eine Altersgruppierung. Das einzig objektive Kriterium ist das chronologische Alter, obwohl derartig definierte Gruppen ebenfalls sehr heterogen sind. An Hand von Untersuchungen an 44 Schädeln mit bekanntem Alter wurde eine Methode zur Bestimmung des Alters entwickelt. Von einem festen Geburtszeitpunkt aller Wiesel am 1. Juni ausgehend, kann das Material zunächst an Hand des Fangmonats und im weiteren aus einer Kombination von mehreren Merkmalen (in erster Linie postorbitale Einschnürung des Schädels) in Gruppen einjähriger und zweijähriger Tiere eingeordnet werden. Ältere Individuen unbekannten Alters können – falls erforderlich – von zweijährigen an dem Abnutzungsgrad der Reißzähne unterschieden werden. Die Ergebnisse aus dieser Methode (nach den drei wichtigsten Bestimmungskriterien „Date-Skull-Baculum (DSB)-Verfahren" genannt) werden mit denen verglichen, welche sich bei Anwendung anderer Bestimmungsmethoden ergeben. Welche Methode die geeignetste ist, hängt von der Größe und dem Fangdatum der Stichprobe ab. Für große Stichproben aus einem Gebiet zeigt sich, wenn sie hauptsächlich im Sommer oder Herbst eingefangen wurden, die DSB-Methode als befriedigend; für kleine oder heterogene Proben ist die Suturen-Methode die beste.

References

ANDERSON, E. (1970): Quaternary evolution of the genus *Martes* (Carnivora, Mustelidae). Acta Zool. Fennica 130, 1–132.

BEAUCOURNU, J. C.; GRULICH, I. (1968): A propos de la belette de Corse. Mammalia 32, 341–371.

BARBU, P. (1968): Systematique et écologie de la belette *Mustela nivalis* L., provenant de quelques forêts des districts d'Ilfov et de Prahova-Roumania. Travaux du Museum d'histoire naturelle "Grigore Antipa" 8, 991–1002.

BELL, G. H. (1956): Bone as a mechanical engineering problem. In: The biochemistry and physiology of bone. Ed. by G. H. BOURNE pp. 27–52. New York: Academic Press.

BOISE, C. M. (1975): Skull measurements as criteria for ageing fishers. N. Y. Fish and Game J. **22**, 32–37.

BREE, P. J. H. VAN; JENSEN, B.; KLEIJN, L. K. J. (1966): Skull dimensions and the length-weight relation of the baculum as age indications in the common otter. Danish Review of Game Biology 4, 97–104.

BUCHALCZYK, T.; RUPRECHT, A. L. (1977): Skull variability of *Mustela putorius* Linnaeus 1758. Acta Theriol. **22**, 87–120.

CHAINE, J. (1926): L'os penien: etude descriptive et comparative. Actes. Soc. Linn. de Bordeaux **78,** 5–195.

CORBET, G. B.; SOUTHERN, H. N. (eds.)(1977): The Handbook of British Mammals, 2nd ed. Oxford: Blackwell Scientific Publications.

DAGG, D. I.; LEACH, D.; SUMNER-SMITH, G. (1975): Fusion of the distal femoral epiphysis in male and female marten and fisher. Can. J. Zool. **53,** 1514–1518.

DEANESLY, R. (1944): The reproductive cycle of the female weasel (*Mustela nivalis*). Proc. Zool. Soc. (Lond.) **114,** 339–349.

DIDIER, R. (1947): Etude systematique de l'os penien des Mammiferes: Carnivores. Famille des Mustelides. Mammalia **11,** 30–43.

ELDER, W. H. (1951): The baculum as an age criterion in mink. J. Mammalogy **32,** 43–50.

FOG, M. (1969): Studies on the weasel (*Mustela nivalis*) and the stoat (*Mustela erminea*) in Denmark. Danish Review of Game Biology **6,** 1–14.

GREER, K. R. (1957): Some osteological characters of known-age ranch minks. J. Mammalogy **38,** 319–330.

HALL, E. R. (1951): American weasels. Univ. Kansas, Mus. Nat. Hist. Publ. **4,** 1–466.

HAMILTON, W. J. (1933): The weasels of New York. Amer. Midl. Nat. **14,** 289–344.

HANSSON, I. (1968): Cranial helminth parasites in species of Mustelidae. I. Frequency and damage in fresh mustelids from Sweden. Oikos **19,** 217–233.

— (1970): Cranial helminth parasites in species of Mustelidae. II. Regional frequencies of damage in preserved crania from Denmark, Finland, Sweden, Greenland and the NE of Canada compared with the helminth invasion in fresh mustelid skulls from Sweden. Ark. Zool. **22,** 571–594.

HEIDT, G. A. (1970): The least weasel, *Mustela nivalis* L; Developmental biology in comparison with other North American *Mustela*. Mich. State Univ., Publ. Mus. (Biol. Ser.) **4,** 227–282.

HENSEL, R. (1881): Craniologische Studien. Nova Acta d. Ksl. Leop-Carol. Deut. Akad. d. Nat. **42,** 127–195.

HILL, M. (1939): The reproductive cycle of the male weasel (*Mustela nivalis*). Proc. Zool. Soc. Lond. (Ser. B.) **109,** 481–512.

JEFFERIES, D. J.; PENDLEBURY, J. B. (1968): Population fluctuations of stoats, weasels and hedgehogs in recent years. J. Zool. Lond. **156,** 513–517.

KING, C. M. (1975): The home range of the weasel (*Mustela nivalis*) in an English woodland. J. Anim. Ecol. **44,** 639–658.

— (1977): The effects of the nematode parasite *Skrjabingylus nasicola* on British weasels (*Mustela nivalis*). J. Zool. Lond. **182,** 225–249.

— (1980): The population biology of the weasel (*Mustela nivalis*) on British game estates. Holarctic Ecol. **3.**

KING, C. M.; EDGAR, R. L. (1977): Techniques for trapping and tracking stoats (*Mustela erminea*); a review, and a new system. N. Z. J. Zool. **4,** 193–212.

KLEBANOVA, E. A.; KLEVEZAL', G. A. (1966): Stratification of the periosteal zone of long bones as a criterion for determining the age of mammals. Transl. by British Lending Library, Boston Spa, Yorks, Translation number RTS 3647. Zool. Zh. **45**; 406–413.

KLEVEZAL', G. A.; KLEINENBERG, S. E. (1967): Age determination of mammals by layered structure in teeth and bone. Transl. by Fisheries Research Board of Canada. Ed. by D. E. SERGEANT. Translation series No. 1024. Akad. Nauk, SSSR, Inst. Morfologii: publ. by Izdatel'stvo "Nauka", Moscow, pp. 144.

LEACH, D. H.; HALL, B. K.; DAGG, A. I.: Aging marten and fisher by development of the suprafabellar tubercle. Can. J. Zool. (in press).

LECHLEITNER, R. R. (1954): Age criteria in mink, *Mustela vison*. J. Mammalogy **35,** 496–503.

LOCKIE, J. D. (1966): Territory in small carnivores. Symp. Zool. Soc. Lond. **18,** 143–165.

MAL'DZHYUNAITE, S. A. (1957): Age determination and age structure of pine martens in Lithuania. In: Biology of Mustelids: some Soviet research. Ed by C. M. KING. pp. 132–144. Boston Spa: British Lending Library 1975.

MAZAK, V. (1963): Eruption of permanent dentition in the genera *Mustela* Linnaeus 1758, and *Putorius* Cuvier 1817, with a note on the genus *Martes* Pinel 1792 (Mammalia, Mustelidae). Vest. Cesk. spol. Zool. **27,** 328–334.

MORRIS, P. A. (1972): A review of mammalian age determination methods. Mam. Rev. **2,** 69–104.

OTERO, J. G.; DAPSON, R. W. (1972): Procedures in the biochemical estimation of age of vertebrates. Res. Popul. Ecol. **13,** 152–160.

PELTON, M. R. (1970): Effects of freezing on weights of cottontail lenses. J. Wildl. Mgmt. **34,** 205–207.

PETROV, O. V. (1956): Sexual dimorphism in the skull of *Mustela erminea* L. In: Biology of Mustelids: some Soviet research. Ed. by C. M. KING. pp. 55–78. Boston Spa: British Lending Library 1975.

POHL, L. (1909): Ueber das Os Penis der Musteliden. Jena Z. Nat. Wissenschaft **45,** 381–394.

— (1910): Wieselstudien. Zool. Beobacht. **51,** 234–241.

POPOV, V. A. (1943): A new age index in Mustelinae. C. R. Acad. Sci. URSS **38,** 258–268.

PUCEK, Z.; LOWE, V. P. W. (1975): Age criteria in small mammals. In: Small Mammals: their productiv-

ity and population dynamics. Ed. by F. B. GOLLEY, K. PETRUSEWICZ and L. RYSZKOWSKI. pp. 55–72. Cambridge: Cambridge University Press.
REINWALDT, E. (1959): Bemerkungen zur Entwicklung und zur taxonomischen Bewertung der Crista sagittalis bei Musteliden. Z. Säugetierkunde **24**, 46–53.
SERGEANT, D. E. (1967): Age determination of land mammals from annuli. Z. Säugetierkunde **32**, 297–300.
SIMKISS, K. (1975): *Bone and biomineralisation. Institute of Biology, Studies in Biology* **53**, 1–60. London: Edward Arnold.
SOEST, R. W. M. VAN; BREE, P. J. H. VAN (1970): Sex and age composition of a stoat population (*Mustela erminea* Linnaeus 1758) from a coastal dune region of the Netherlands. Beaufortia **17**, 51–77.
SPINAGE, C. A. (1973): A review of the age determination of mammals by means of teeth, with especial reference to Africa. E. Af. Wildl. J. **11**, 165–187.
STEARNS, S. C. (1977): The evolution of life-history traits: a critique of the theory and a review of the data. Ann. Rev. Ecol. Syst. **8**, 145–171.
STEENKAMP, J. D. G. (1975): Guidelines to the use of dental histology in wildlife research. J. Sth. Af. Wildl. Mgmt. Ass. **5**, 89–94.
STROGANOV, S. U. (1937): A method of age determination and an analysis of the age structures of ermine populations (*Mustela erminea* L.) In: Biology of mustelids: some Soviet research. Vol. 2. Ed. by C. M. KING. Wellington, New Zealand: Department of Scientific and Industrial Research. (*in* press).
STUBBE, M. (1969): Populationsbiologische Untersuchungen an *Mustela* – Arten. Hercynia **6**, 306–318.
VERSHININ, A. A. (1972): The biology and trapping of the ermine in Kamchatka. In: The Biology of Mustelids: some Soviet research. Vol. 2. Ed. by C. M. KING. Wellington, New Zealand: Department of Scientific and Industrial Research. (in press).
WALKER, D. R. G. (1972): Observations on a collection of weasels (*Mustela nivalis*) from estates in southwest Hertfordshire. J. Zool. Lond. **166**, 474–480.
WALTON, K. C. (1968): The baculum as an age indicator in the polecat *Putorius putorius*. J. Zool. Lond. **156**, 533–536.
WRIGHT, P. L. (1947): The sexual cycle of the male long-tailed weasel (*Mustela frenata*). J. Mammalogy **28**, 343–352.
— (1950): Development of the baculum of the long-tailed weasel. Proc. Soc. Exp. Biol. and Med. N. Y. **75**, 820–822.

Author's address: Dr. CAROLYN M. KING, 3 Waerenga Road, Eastbourne, New Zealand