Nutritional Factors Regulating Deer Antler Development and Regeneration: Postprint

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Abstract

Deer antler velvet is a traditional Chinese medicine with high medicinal value. As a secondary sexual characteristic of male deer, antler generation and regeneration are regulated not only by hormones but also closely related to nutritional factors. Nutritional factors significantly influence pedicle formation, first antler generation, and antler development. This review summarizes research findings over the years on the effects of nutritional factors on antler generation and regeneration, analyzes the pathways through which nutritional factors regulate pedicle and antler generation and development, and proposes that nutritional factors regulate antler generation and regeneration via direct and indirect pathways.

Full Text

Regulation of Antler Initiation and Regeneration by Nutritional Factors

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Abstract: Antler, a traditional Chinese medicine with high medicinal value, represents a secondary sexual characteristic in male deer. The processes of antler initiation and regeneration are regulated not only by hormones but also closely associated with nutritional factors. Nutrition exerts substantial influence on pedicle formation, first antler initiation, and antler development. This review synthesizes research findings on nutritional effects on antler initiation and

regeneration, analyzes the pathways through which nutrition regulates pedicle and antler development, and proposes that nutritional factors control antler initiation and regeneration through both direct and indirect mechanisms.

Keywords: nutritional factors; antler initiation; antler regeneration; regulatory pathways

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Antler is recognized as the only mammalian organ capable of complete regeneration and among the fastest-growing animal tissues. Antler initiation and regeneration occur seasonally, once annually. The process begins in spring when the pedicle develops from the frontal crest on the deer' s skull. Upon pedicle completion, the first antler forms at the pedicle apex. During summer, the first antler grows rapidly, ossifying in autumn. The following spring, the first antler is cast from the pedicle, marking the start of antler regeneration. The regenerated antler, termed "replacement antler," develops rapidly in summer and ossifies in autumn. This cycle repeats annually. While the first antler and replacement antlers are temporary structures, the pedicle is permanent.

Antler initiation and regeneration are strictly regulated by hormones [1-5]; however, nutritional factors represent a critical determinant of whether antlers initiate on schedule and enter the regeneration cycle. Understanding the regulatory factors in antler development and the pathways of nutritional regulation provides theoretical foundations for manipulating antler development through nutritional management to enhance antler yield and quality.

1. Nutritional Regulation of Antler Initiation

Antler initiation originates from the antlerogenic periosteum (AP). In most deer species, when animals reach puberty (5-7 months in red deer), the AP gradually develops into a pedicle, whose apex then forms the first antler. Beyond sex hormones, pedicle and first antler initiation are strictly controlled by nutritional factors.

1.1 Relationship Between Nutrition and Pedicle Development

Puberty marks the specific period for pedicle initiation, which requires two conditions [1]: first, the onset of puberty with rising plasma testosterone levels [2-5]; second, attainment of a species-specific body weight threshold [6-7], referred to herein as the "pedicle initiation weight threshold."

The timing at which an individual reaches this threshold depends primarily on nutritional status. Well-nourished male red deer fawns achieve the pedicle initiation weight threshold earlier, resulting in earlier pedicle initiation [8]. Conversely, deer under poor nutritional conditions experience delayed threshold attainment and consequently delayed pedicle initiation. For example, when male red deer fawns were fed 70% of normal dietary requirements, pedicle initiation was delayed by 12 weeks compared to ad libitum-fed individuals; however, once

these restricted deer reached the weight threshold, pedicle initiation proceeded immediately [7]. In cases of severe nutritional deficiency, pedicle initiation may be delayed by a year or more [9]. Male red deer that fail to produce antlers, termed "hummels," result from malnutrition that prevents pedicle formation or causes incomplete pedicle development, rendering them incapable of antler production [1].

Pedicle initiation originates from proliferation of AP tissue cells. Li et al. [10] systematically studied red deer AP tissue structure, finding that AP thickness and cell density correlate with nutritional status—well-nourished deer exhibit greater AP thickness and higher cell density. Histological comparisons during pre-pedicle initiation revealed that AP tissue in normal male fawns was thicker than in hummels, particularly in the cell layer [1]. These findings demonstrate that poor nutrition limits AP cell proliferation, and the pedicle initiation weight threshold serves as an indicator of nutritional status. Once deer reach this threshold, AP cells proliferate, the pedicle begins developing, and this mechanism explains why pedicle initiation requires attainment of the weight threshold.

1.2 Pedicle Initiation Weight Threshold is Species- and Region-Specific

The pedicle initiation weight threshold varies among deer species in the same region and even among populations of the same species in different regions. Red deer have been most extensively studied in this regard, primarily because they are among the most widely distributed deer species and show substantial variation in average body weight across regions [11]. Reported thresholds for red deer range from 41-56 kg [6-7]. Scottish red deer, the world' s smallest subspecies, average 100 kg [8,11]. Genetically, Scottish red deer possess the potential for larger body size, but poor vegetation and food scarcity limit juvenile development, preventing attainment of their genetic potential [8]. Consequently, their pedicle initiation weight threshold is the lowest reported at 41 kg [7]. Fennessy et al. [6] determined the threshold for New Zealand red deer to be 56 kg, the highest documented value.

Regional variation in red deer average weight primarily reflects nutritional differences arising from geographic and environmental conditions affecting food availability [11]. We hypothesize that the pedicle initiation weight threshold correlates with regional adult body weight. If valid, we propose using a "pedicle initiation index" (the ratio of the regional threshold to average adult weight) to evaluate the relationship between pedicle initiation and body weight while controlling for regional variation. For example, Scottish red deer have an index of 0.41 (41/100), suggesting New Zealand red deer should have a similar index (56/X), yielding a theoretical average weight of 136 kg for that population. The accuracy of this index requires extensive validation and large-scale statistical analysis.

The existence of a pedicle initiation weight threshold indicates that deer assess

their body weight to determine whether sufficient nutrients are available to support pedicle and first antler development. Body development takes priority over antler development [8]. Under poor nutrition, all nutrients support body growth and maintenance until the weight threshold is reached; only then can surplus nutrients be allocated to pedicle development. These nutrients ultimately act on AP cells, triggering proliferation and pedicle initiation [12]. Under adequate nutrition, fawns reach the threshold before puberty, AP cells receive sufficient nutrients, and pedicle development begins at the normal time.

1.3 Relationship Between Nutrition and Initial Antler Development

When the pedicle reaches species-specific height (5-6 cm in red deer, ~3.5 cm in reindeer) [6,13], the first antler initiates at its apex. This species-specific pedicle length at first antler formation is termed the "initial antler pedicle length threshold."

Like pedicle initiation, first antler timing is constrained by nutrition. Delayed pedicle initiation inevitably delays first antler formation [6]. Under adequate nutrition, male fawns produce first antlers immediately upon pedicle completion; poor nutrition postpones this process. For example, malnourished red deer fawns may delay first antler formation until 2-3 years of age due to incomplete pedicle development [1,9]. Suttie et al. [8] fed Scottish red deer fawns different nutritional levels, finding that high-nutrition groups (FWH) initiated first antlers earlier (reached pedicle length threshold sooner), grew faster, and produced heavier antlers at velvet shedding than low-nutrition groups (FWL) (Table 1). Additionally, high-nutrition groups showed branching in first antlers (Table 2), demonstrating that nutrition affects not only initiation timing but also branching patterns, as most deer species typically produce unbranched first antlers.

2. Nutritional Regulation of Antler Regeneration

While nutrition controls antler initiation, research on nutritional regulation of antler regeneration remains limited. Most studies focus on nutritional effects during initiation and on antler growth, structure, and composition. This gap exists for two reasons: first, cervids are the only animals that produce bony antlers, precluding cross-species data borrowing; second, antlers are integral body components whose metabolism cannot be easily isolated from whole-body metabolism [14-15].

Current evidence indicates that, unlike initiation, nutrition primarily affects antler growth rate rather than regeneration cycle timing. Suttie et al. [7] found that replacement antler cycles in male red deer correlate closely with photoperiod, not body weight. Fennessy et al. [6] fed 2-year-old male red deer low-protein diets during winter (the antler development period), finding both antler and subsequent cast antler weights lower than in high-protein groups (Table 3). In 4-year-old males fed different nutritional levels during the first 65 days of

antler regeneration, low-nutrition groups showed slower antler growth (Table 4). These results demonstrate that nutrition affects replacement antler growth rate.

From an evolutionary perspective, these differences are understandable. During antler initiation, male fawns are in puberty, where body development is the primary physiological priority for survival. When nutrition is limited, nutrients are allocated to body growth first. Only after meeting body development needs can surplus nutrients initiate pedicle and antler formation. In contrast, regenerating males have passed puberty and possess the physical capacity to support antler development, making the regeneration cycle less strictly nutrition-dependent. Although nutrition can influence regeneration timing, this effect is minimal. Fennessy et al. [6] showed that winter nutrition affected antler casting time but not the casting event itself, indicating no impact on regeneration initiation (Table 5). This represents a quantitative rather than qualitative limitation, unlike the "all-or-nothing" constraint of the pedicle initiation weight threshold.

3. Pathways of Nutritional Regulation of Pedicle and Antler Development

Nutrition regulates pedicle and antler initiation timing, first antler branching patterns, and antler growth rate. The mechanisms underlying these effects have long been debated. The most widely accepted theory is the "insulin-like growth factor-1 (IGF1) hypothesis" [1,6,16-17]. IGF1 is a crucial regulator of growth, development, and metabolism that activates RNA polymerase, promotes non-histone phosphorylation, stimulates RNA and DNA synthesis, and enhances cell growth and division. IGF1 also improves amino acid utilization in protein synthesis, inhibits protein degradation, increases net protein accretion, and promotes osteoblast and myoblast proliferation, thereby facilitating embryonic development, bone growth and repair, and muscle growth. Serum IGF1 levels serve as an important indicator of nutritional metabolism, as IGF1 synthesis, release, and activity depend on nutritional status. Therefore, nutrition primarily influences antler development by elevating plasma IGF1 peaks, thereby regulating antler growth rate.

3.1 Direct Pathway

Plasma IGF1 levels change systematically during pedicle and first antler development in male red deer [6] (Table 6), showing seasonal patterns that parallel antler (including replacement antler) growth rates. Suttie et al. [16] identified a plasma IGF1 peak during pre-pedicle formation that may serve as the initiation signal. Reindeer, the only deer species where females also produce antlers, show higher plasma IGF1 levels in males than females during the pedicle and first antler period (0-21 weeks) [13], correlating with antler length differences (Figure 1 [Figure 1: see original paper]). The timing of IGF1 peaks coincides with periods of maximum antler growth rate.

Cellular studies confirm IGF1 promotes antler development. *In vitro* proliferation of mesenchymal and chondrocyte cells from the antler growth zone (collectively termed growth center cells) depends on IGF1 concentration, with maximum sensitivity at 60 days post-casting [4]. IGF1 stimulates proliferation of antler tip cells and regenerating antler growth zone cells in serum-free culture [18] and dose-dependently stimulates AP cell proliferation [3]. These findings demonstrate that IGF1 directly acts on AP cells and antler growth center cells, inducing proliferation and driving pedicle development and rapid antler growth.

The correlation between antler growth rate and plasma IGF1 levels relates to nutrition in three ways: (1) both rapid antler growth and IGF1 peaks occur during summer when food is abundant; (2) nutritional studies show that slow antler growth in low-nutrition 4-year-old red deer accompanies low plasma IGF1 [6], and sika deer plasma IGF1 trends match dietary digestible protein levels, decreasing during chronic malnutrition [19-20]; (3) studies in other animals confirm a causal relationship between nutrition and plasma IGF1, with nutrition being a primary regulator of IGF1 levels [21-24]. Thus, nutrition directly controls pedicle and antler initiation and rapid growth by influencing IGF1 peak levels.

3.2 Indirect Pathway

Beyond direct control via IGF1, nutrition indirectly regulates pedicle and antler development by modulating body weight through IGF1. Numerous studies demonstrate that male deer body weight directly affects antler weight and size, with larger individuals typically bearing larger antlers [25-26].

The pedicle initiation weight threshold provides clear evidence of body weight control over pedicle development. The relationship among nutrition, body weight, and antler size manifests before pedicle initiation. Suttie et al. [27] conducted restricted feeding trials on captured wild red deer and Scottish red deer fawns: (1) wild male fawns fed different dietary levels from their first winter showed reduced feed intake (Figure 2 [Figure 2: see original paper]) and lower body weight (Figure 2); (2) Scottish red deer fed different nutritional levels at 23-46 weeks of age (first winter) showed weight gain dependent on nutrition, with poorly nourished deer being smaller and lighter (Table 1). These restricted feeding trials resulted not only in lower body weight but also smaller first antler length (Figure 3 [Figure 3: see original paper]) and weight (Table 2). Gaspar-López et al. [28] confirmed that Iberian red deer first antler size and weight correlate strongly with body weight at 6 months (before pedicle formation), with heavier deer producing longer, heavier antlers. This pre-antler period represents a critical growth window; nutritional deficits that affect body weight cannot be compensated later [8,29]. Hummels' inability to produce antlers stems primarily from poor juvenile nutrition [1].

3.3 Relationships Among Antler, Body Weight, and Nutrition

The relationship between antlers, body weight, and nutrition reflects their positive correlation. Cast antler weight in red deer shows linear positive correlation with body weight (Figure 4 [Figure 4: see original paper]) [4]. Within age groups, antler length and body weight are positively correlated, with heavier deer producing significantly longer antlers [31]. Stewart et al. [32] similarly found significant correlation between moose body weight and antler size, hypothesizing that because antler growth requires substantial nutrients, larger individuals can acquire more nutrients, leaving surplus for rapid antler growth beyond body maintenance.

While genetics primarily determine interspecies differences in body weight and antler size/shape, intraspecific variation appears more nutritionally than genetically mediated. Hummels' antlerlessness results from poor juvenile nutrition rather than genetics (their offspring can produce antlers normally) [1]. Foerster et al. [25] evaluated genetic selection effects on red deer antler development over 30 years, finding no clear positive correlation between antler size and genetically determined body size. Thus, genetic variation in body weight may minimally affect antler development.

Suttie et al. [16] studied plasma IGF1, body weight, and antler growth in 4-15-month-old red deer males, finding that plasma IGF1 patterns (Figure 5 [Figure 5: see original paper]), body weight gain, and antler growth rate were synchronized and positively correlated. Li et al. [33] administered exogenous testosterone to castrated males, normal adult females, and freemartin red deer to stimulate antler growth. Under testosterone stimulation: (1) pedicle and first antler growth rates (Figure 6 [Figure 6: see original paper]) and body weight changes (Figure 7 [Figure 7: see original paper]) paralleled plasma IGF1 levels (Figure 7); (2) antler-producing females and freemartins had higher plasma IGF1 than non-antlered controls. These experiments establish causality: elevated plasma IGF1 drives increased body weight and rapid antler growth during the antler production period.

A notable exception involves roe deer, where antler weight-body weight correlations vary regionally [26]. This likely reflects that roe deer antlers are small, lack commercial value, and all data come from wild animals (often hunted). Wild roe deer face more complex environments than farmed or grazing deer, with vegetation nutrient content varying by geography and climate. Thus, nutrition affects antler development through both pathways; when direct regulation dominates, antler weight correlates less with body weight, and vice versa.

3.4 Relationships Among Nutrition, IGF1, Testosterone, and the Antler Cycle

Although nutrition cannot alter the antler regeneration cycle, it influences velvet shedding and antler casting times. In Scottish red deer fed different nutritional levels at 23-46 weeks of age, high-nutrition groups showed earlier velvet shedding:

by autumn slaughter, 3/7 had clean cast antlers, 1/7 were shedding, and 3/7 remained in velvet; low-nutrition groups had only 1/7 shedding and 4/7 still in velvet [8]. Fennessy et al. [6] demonstrated nutrition' s effect on casting time: restricted feeding delayed velvet shedding by 8 weeks compared to high-nutrition groups, and winter supplementary feeding advanced casting time in four deer farms (Table 5). Muir et al. [30] confirmed this effect in 3-9-year-old red deer, showing winter supplementation advanced casting time.

Testosterone and IGF1 both play important but distinct roles in antler formation [6]. The antler initiation and regeneration cycle is testosterone-controlled (e.g., velvet shedding is triggered by high plasma testosterone), while rapid antler growth is primarily IGF1-controlled [18]. In restricted feeding trials, high-nutrition Scottish red deer not only shed velvet earlier but also had larger testes than low-nutrition deer [8]. At the cellular level, AP cells respond to testosterone only in the presence of IGF1, with IGF1 effects being dose-dependent [1]. The collective evidence shows correlations among nutrition, plasma testosterone, and IGF1 levels, with nutrition significantly affecting velvet shedding, antler casting, and antler growth rate. We hypothesize that nutrition influences plasma IGF1 levels, which in turn affect testosterone levels, thereby modulating velvet shedding and antler casting times.

Based on these findings, we propose the following causal relationships: nutrition regulates antler development through two mechanisms—direct action via IGF1 and indirect action through IGF1-mediated effects on body weight. This hypothesis explains why nutritionally rather than genetically determined body weight differences regulate antler development, as nutrition drives plasma IGF1 variation.

Further research into nutritional effects on antler development and the molecular mechanisms of endocrine regulation of rapid antler growth will not only enhance antler production but also provide insights into promoting rapid tissue repair through nutrition rather than drugs, ultimately benefiting human health.

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Note: Figure translations are in progress. See original paper for figures.