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Notes

Food Handling and D1 Unguis in the White-tailed Antelope Squirrel

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***Abstract.*—It has been shown recently that rodent species that feed orally (reaching towards the food with the mouth) lack a D1 digit, whereas species that feed oromanually (holding the food with the forepaws) have a nail or claw on D1, a nail being more common than a claw. I determined that the White-tailed Antelope Squirrel (*Ammospermophilus leucurus*) conforms to the predominant rodent combination of oromanual feeding pattern and the presence of a D1 digit but has a D1 appendage intermediate between a nail and a claw. This finding is important because it adds nuance to the general rule of forepaw morphology and food handling in rodents.**

Key Words.—*Ammospermophilus leucurus*; integumental skeleton; morphology; oromanual feeding.

The keratinized integument of mammals (the unguis) includes nails, which are keratinized plates on the dorsal surface of a digit, claws, which are laterally compressed structures that protrude over the tip and the dorsolateral surface of the digit, and hoofs, which are enlarged keratinized appendages typical of ungulates (Krejsa 1979). A recent comparative study provided evidence that, at least within the order Rodentia, there may be an association between the food handling strategy employed by the members of the species and the type of keratinized integument of the first digit (D1 or thumb) of the front paw (Missagia et al. 2025). Thus, species that feed orally (reaching towards the food with the mouth) lack a D1 unguis, whereas species that feed oromanually (holding the food with the forepaws) have a nail or claw on D1, a nail being more common than a claw.

The study by Missagia et al. (2025) made use of archival photographs of feeding behavior and examination of museum specimens. Because I had a colony of White-tailed Antelope Squirrels (*Ammospermophilus leucurus*) in my laboratory, I decided to evaluate the general principle in this specific species with real-time data. The White-tailed Antelope Squirrel is indigenous to a large segment of western North America, from as far north as southern Idaho and Oregon (43°N) to as far south as the tip of the Baja California peninsula (23°N; Belk and Smith 1991; Koprowski et al. 2016). I report here that the White-tailed Antelope Squirrel conforms to the usual rodent combination of oromanual feeding pattern and presence of a D1 digit but has a D1 appendage intermediate between a nail and a claw.

I obtained 24 adult White-tailed Antelope Squirrels, half of each sex, from a larger colony of animals born in captivity to pregnant females that I had caught in Owyhee County, Idaho. The animals were fully grown at the time of the study and weighed an average of 120 g. I housed the animals individually, because they are solitary (Belk and Smith 1991), in polypropylene cages with wire tops (36 cm length, 24 cm width, 19 cm height) with access to a running wheel (15 cm diameter) for environmental enrichment. I lined the cages with wood bedding and squirrels were kept inside individual light-tight, ventilated, individual chambers under a light-dark cycle with 12 h of light per day (360 lux) and constant ambient temperature of 26° C. I provided them with Purina rodent chow (Rodent Diet 5001, Lab Diet, St. Louis, Missouri) and drinking water *ad libitum*.

For observation of food handling, I handed each squirrel a single almond nut at noon twice a week and I observed each squirrel for 2 min. I made observations over 6 mo. Following the procedures of Missagia et al. (2025), I defined oral-only feeding as a feeding pattern that generally involves only the orofacial apparatus, with no forepaw-holding of the food, whereas I defined oromanual feeding as a feeding pattern that clearly involves forepaw-holding of the food. After the observations of food handling were completed, I used squirrels in a separate study (unpubl. data), at the end of which they were euthanized. I examined forepaws *post mortem* with a focus on the unguis of each digit with and without a stereo microscope. For comparative purposes, I also examined photographs of the forepaws of four pet Common Marmosets (*Callithrix jacchus*; average body weight 260 g).

I considered an unguis to be a claw if it protruded dorsally and distally with a substantial overhang, and the overhanging portion tapered to a pointy tip and curved downward to form a hook-like structure (Missagia et al. 2025). In contrast, I considered an unguis a nail if it had little or no overhang and had a blunt distal edge. Additionally, I expected a claw to be longitudinally curved and laterally compressed, whereas I expected a nail to be thin and relatively flat.

All animals ate rodent chow regularly. Because of the design of the cages, the chow pellets had to be reached with the mouth; however, I offered almonds directly to

Figure 1. Typical posture of a White-tailed Antelope Squirrel (*Ammospermophilus leucurus*) holding an almond in its forepaws while eating. (Photographed by Roberto Refinetti).

the squirrels, and they were able to hold the almond in their forepaws while eating it. Twenty of the 24 squirrels exhibited anticipatory activity when I approached the cage with the almond. Squirrels seized the almond with their mouth quickly and immediately grasped it with their forepaws to eat it (Fig. 1). Seizing of the almond with the mouth was too brief for detailed examination but seemed to involve a simple grabbing of the nut with the lips without exposing the teeth. The four squirrels that did not show anticipatory activity allowed the almond to fall to the bottom of the cage instead of seizing it with the mouth but reached for the almond orally a few seconds later and held it in the forepaws while eating it. Occasionally, the squirrels ate part of the almond and stored the remaining part in the cheek pouch. For additional documentation, many photographs on the iNaturalist website (https://www.inaturalist.org/taxa/46255-Ammospermophilus-leucurus/browse_photos) show oromanual food handling by White-tailed Antelope Squirrels in the wild.

Post mortem examination of the forepaws revealed the common arrangement of digits in rodents: four large digits (D2 through D5) and a rather small thumb (D1). The four large digits clearly had unguis of the claw type, whereas D1 had a less clear unguis. Viewed from the dorsal surface, D1 seemed to have a claw, but the unguis resembled more of a nail when viewed from the volar surface (Fig. 2). Closer examination under a stereo microscope indicated the D1 unguis to have the curvature of a claw but the thin plate typical of a nail (Fig. 3). Despite this ambiguity, it was evident in all squirrels examined that the hand had a noticeable D1 digit and that the digit had a short but conspicuous keratinized structure. In comparison to the intermediate unguis in these terrestrial squirrels, the D1 unguis in the arboreal marmoset was clearly a claw, as noticeable in a view of the whole hand and unequivocal in a close-up view (Fig. 4).

Because the squirrels were raised in the laboratory, there is a possibility that the unguis grew longer than in the field because they were not worn down by abrasion, which is known to occur in zoo animals (https://zooatlanta.org/trim-your-toes/). To exclude this possibility, I inspected photographs of White-tailed Antelope Squirrels living in the wild in the iNaturalist website (Fig. 5). The D1 unguis of the hand is not visible in these or any of the other photographs available on the website, but the unguis of the other four digits are clearly similar to those of the squirrels raised in the laboratory and do not evince greater wear under field conditions.

The behavioral observations in this study revealed a clear oromanual food handling strategy in White-tailed Antelope Squirrels. Examination of the forepaws also revealed a clear pattern with four large digits and a small thumb. This combination of food handling strategy and finger pattern is consistent with that described as the most common in rodents (Missagia

Figure 2. (A) Dorsal and (B) volar views of the front paws of White-tailed Antelope Squirrel (*Ammospermophilus leucurus*). Each digit is identified by its digit number. Scale bar: 5 mm. (Photographed by Roberto Refinetti).

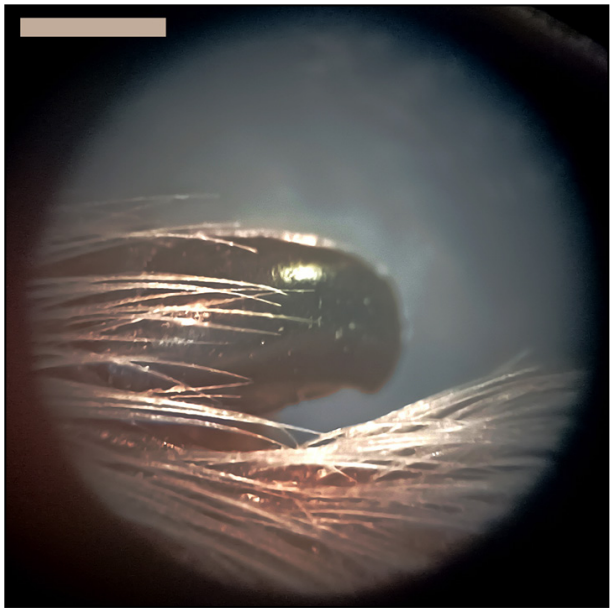

Figure 3. View of the D1 unguis of a White-tailed Antelope Squirrel (*Ammospermophilus leucurus*) under a stereo microscope. Scale bar: 1 mm. (Photographed by Roberto Refinetti).

et al. 2025). The distinction between nail and claw, however, was not as clear.

The ambiguity in the keratinized integument of D1 may be a feature of the evolutionary process in squirrels. The presence of a nail on D1, which is more common than a claw in the order Rodentia (Missagia et al. 2025), is not a requirement for the oromanual food handling strategy, which is evident from the fact that marmosets, unlike most primates, have claws on D1 (Soligo and Smaers 2016) but also have excellent manual dexterity (Bertrand et al. 2025), which is an ancestral primate feature (Bloch and Boyer 2002). The presence of a nail or a claw in D1 may not be of much relevance, considering that the claws of the Domestic Mouse (*Mus musculus*) share major physical characteristics with human nails (Fleckman et al. 2013). Also, the broad analysis by Missagia et al. (2025) did indicate several exceptions to the oromanual-nail association as well as the existence of various cases of ambiguous unguis type that they designated as intermediate between nail and claw. Thus, the important finding of my study is the confirmation of the combination of food handling strategy (oromanual feeding) and hand pattern (four large clawed digits and a small thumb with a nail or short claw) in a species of *Ammospermophilus*.

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Figure 4. (A) Full and (B) magnified view of the forepaw of a Common Marmoset (*Callithrix jacchus*). Each digit is identified by its digit number. (Photographed by Roberto Refinetti).

Figure 5. Forepaws of White-tailed Antelope Squirrels (*Ammospermophilus leucurus*) living in the wild in (A) Lander County, Nevada, (B) Riverside County, California, and (C) San Diego County, California. The images were cropped from photographs posted on the iNaturalist database (https://www.inaturalist.org/taxa/46255-Ammospermophilus-leucurus/browse_photos).

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