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Article

# Endozoochory by Goats and White-Tailed Deer: Type of Ruminant Affect Recovery and Germination of *Neltuma pallida* Seeds

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## Abstract

The “algarrobo”, *Neltuma pallida* is a key tree species in the seasonally dry tropical forests in Equatorial Pacific South America, currently at risk. Its regeneration depends on endozoochorous seed dispersal, in which seeds are ingested and later defecated by animals, helping to release and scarify them. This study compared the role of the native white-tailed deer (*Odocoileus virginianus*) and the introduced goat (*Capra hircus*) in seed dispersal. Seeds were recovered from the dung of both species after experimental feeding and from free-ranging goats grazing in fruiting *N. pallida* forests. Seed recovery was higher in deer dung (9.4%) than in goat dung (3.1%). Retention time was also shorter in deer (peak at 48 hours) than in goats (peak at 84 hours). Only deer scarification significantly improved germination percentage (Tukey test,  $p < 0.001$ ) and germination speed ( $T_{25} = 8.98$  days). Goats reduced germination speed under experimental conditions ( $T_{25} = 19.25$  days), but slightly improved it under forest conditions ( $T_{25} = 12.81$  days). These differences are attributed to the morphophysiological traits of each species. Although goats did not enhance overall germination, they maintained it at ~44% and contributed to seed dispersal and dormancy release.

**Keywords:** endozoochory; scarification; ruminant; germination; physical dormancy

## 1. Introduction

The “algarrobo”, *Neltuma pallida* (Humb. & Bonpl. ex Willd.) C.E. Hughes & G.P. Lewis is a tree species within the genus *Neltuma*, which is distributed across the arid and seasonally dry tropical region of South America [1]. *N. pallida* occurs naturally in the arid lowlands along the Pacific coast of Peru, Colombia, and Ecuador, and has been introduced into other regions of the Americas and Asia [2]. It is a keystone species, highly adapted to the variable dry and wet conditions of northern coastal Peru [3] and plays a vital role in sustaining rural livelihoods by providing firewood, charcoal, and forage for livestock [4]. Currently, *N. pallida* population is undergoing a decline due to illegal logging, pest outbreaks, and land-use change [5–7]. It is considered a high-risk genetic resource in South America [8].

Natural forest regeneration depends on seed dispersal, a critical ecological process for habitat colonization and landscape connectivity [9–11]. *N. pallida*, like other species within the genus *Neltuma* (formerly *Prosopis*), is primarily dispersed through endozoochoric [12,13], a form of seed dispersal mediated by animals that involves seed release, scarification, and transportation. The species produces indehiscent legumes with thick seed coats that protect the seeds [14]. Seed release is

essential, as seeds contained in intact pods and deposited on the ground typically fail to germinate [15]. Moreover, *Neltuma* seeds exhibit physical dormancy due to a water-impermeable seed coat [16]; without scarification, germination rates can be lower than 7% for several *Neltuma* species [17].

Among the most important endozoochorous dispersers of *Neltuma* species are wild and domestic herbivorous mammals, which are capable of transporting seeds over long distances [15,18–20]. In the case of *N. pallida* in dry forest ecosystems, this role would historically have been fulfilled by the white-tailed deer (*Odocoileus virginianus*), a remnant of the Neotropical megafauna [21]. However, this species is now highly scarce, mainly due to poaching. Conversely, since the expansion of goat (*Capra hircus*) husbandry in the 18th century [22], goat rearing has become widespread throughout these forests. Currently, in Peru alone, approximately 500,000 goats are raised in these ecosystems.

This shift in ruminant populations may influence the efficiency of *N. pallida* endozoochory. Exotic dispersers can have negative effects on the germination of seeds from native species [23]; even though both species are ruminants, they differ functionally in their feeding strategies. While the white-tailed deer is a concentrate selector (CS), the goat is classified as an intermediate feeder [24]. These feeding types are associated with distinct morphophysiological traits that may influence seed recovery and scarification, potentially altering the natural regeneration dynamics of *N. pallida*.

To date, no studies have evaluated the seed scarification efficiency of *N. pallida* by goats and white-tailed deer. We hypothesize that seed passage through the gastrointestinal tract enhances both the germination rate and percentage of *N. pallida* seeds, and that this effect may be greater when mediated by white-tailed deer. To assess endozoochorous efficiency in goats and deer, we evaluated seed recovery and germination of *N. pallida* through both controlled experiments and grazing trials in dry forest ecosystems.

## 2. Materials and Methods

### 2.1. Location

Two feeding trials for seed scarification were conducted: one under field conditions with grazing goats, and another under controlled feeding conditions with both goats and white-tailed deer. For the grazing trial, a goat herd was selected in the locality of Belén (5° 01'42.9" S, 80° 09'31.41" W; 104 m.a.s.l.), located within the dry forests of Chulucanas, Piura region. The controlled feeding experiments were conducted using enclosures at the Universidad Nacional Agraria La Molina (UNALM) and a fenced area at the "White-tailed Deer" breeding center of the Pontificia Universidad Católica del Perú (PUCP) from May to September 2018.

### 2.2. Fruit Collection and Characteristics

Fruits of *N. pallida* were randomly collected from 40 trees within a 12-hectare relict dry forest in Chulucanas, Piura region, Peru (5° 01' S, 80°09' W; 102 m.a.s.l.) during April 2018. The fruits were stored in a dry environment until the start of the feeding trials, two weeks later. Fruits were characterized by the number of viable seeds per kilogram, as *N. pallida* seeds are rapidly parasitized by bruchid beetles over successive generations [25]. At the time of the experimental feeding, the average weight of a healthy seed was  $38 \pm 6$  mg ( $n = 249$ ), corresponding to an estimated 2,140 viable seeds per kilogram of fruit at the onset of the feeding experiment.

### 2.3. Feeding Trials

Feeding trials with *N. pallida* fruits were conducted using goats and white-tailed deer under confinement conditions in Lima, and with goats under grazing conditions in dry forest areas of Chulucanas, Piura. In the dry forest environment, only goats were used, as the extremely low density of white-tailed deer made it unfeasible to recover a sufficient quantity of seed-containing dung.

Five goats were housed in a shared 40 m<sup>2</sup> pen equipped with a large feeder, ad libitum forage, and water. The three deer were kept within a 150 m<sup>2</sup> fenced enclosure inside the breeding center. The base diet consisted of maize (*Zea mays*) and sorghum (*Sorghum bicolor*) forage for the goat, and alfalfa (*Medicago sativa*) and broad bean pods (*Vicia faba*) for the deer. It was not possible to use the same forage source for both species, as the deer consistently rejected grasses. Both goats and deer underwent a 14-day adaptation period during which they were gradually offered *N. pallida*, increasing from 300 to 700 g/animal. After this period, the pods were removed from the diet, and animals were monitored for an additional 14 days to allow for complete defecation of any ingested seeds.

Finally, animals were fed a single dose of *N. pallida* pods: 940 g for deer (equivalent to 1,900 seeds). Dung were collected at 12-hour intervals over 7 days. To prevent premature seed germination, samples were immediately oven-dried at 48°C (maintaining approximately 40°C at the fecal surface) for 3 hours. The presence of seed in goat and deer dung was recorded daily to estimate the temporal pattern and percentage of seed recovery

#### 2.4. Scarification Treatment

Seeds were recovered from the dung of goat and white-tailed deer (WTD) to evaluate germination performance, in comparison with manually extracted seeds and seeds subjected to physical scarification. The treatments are detailed in Table 1. During seed recovery, two categories of seeds were observed: (1) normal seeds with an appearance identical to the ingested ones, and (2) germinating or degraded seeds, typically black in color and ranging from smooth to wrinkled. For germination trials, only seeds with normal appearance were counted and used (Figure 2).

**Table 1.** Description of treatments used for scarification of *N. pallida*.

Treatment	Type of scarification	Description
Goat	Biological	Seeds recovered from the dung of experimentally fed goats. Only one intake of <i>N. pallida</i> fruits.
Deer	Biological	Seeds recovered from the dung of experimentally fed WTD. Only one intake of <i>N. pallida</i> fruits.
Goat in Dry Forest	Biological	Seeds recovered from the dung of goats grazing in dry forest. Continuous feeding with <i>N. pallida</i> fruits.
Manual release	No treatment	Intact seeds extracted from the fruits, without scarification.
Physical scarification	Physical	Seeds mechanically scarified with sandpaper.

#### 2.5. Germination Experiment

Germination experiment was conducted between June and July 2018 at the Laboratorio de Ecología y Utilización de Pastizales (LEUP) of the Universidad Nacional Agraria La Molina, Peru. All seeds were disinfected by immersion in a 1% sodium hypochlorite solution for 2 minutes, followed by rinsing with distilled water. For each treatment, six 9 cm Petri dishes (replicates) were prepared, each containing 50 seeds. Seeds were placed on layers of filter paper, and moisture was maintained daily using distilled water. Petri dishes were placed in controlled environment germination chambers, set to a photoperiod of 12 h light at 30°C and 12 h dark at 15°C, with constant relative humidity at 70%. A gradual temperature transition between the light and dark periods was programmed to simulate natural dry forest conditions. Germination was monitored daily over 35 days. A seed was considered germinated when the radicle reached a length of 2 mm.



**Figure 1.** (a) Fragments and seeds recovered from WTD dung, (b) Appearance of seeds considered for the germination experiment. (c) Seeds in the process of germination, with signs of inhibition and darkening.

## 2.6. Data Analysis

Seed recovery and germination data were treated as proportions. The temporal dynamics of seed recovery and germination were described using the Morgan-Mercer-Flodin [26], a commonly employed method for modeling cumulative seed recovery and germination curves [15]. This function models sigmoidal cumulative curves (assuming recovery and germination equal to zero at time zero). The model includes three parameters: alpha, gamma, and m. Parameters were estimated using nonlinear least squares.

$$g = \frac{\alpha * t^m}{\gamma + t^m}$$

In the model, g represents cumulative germination, t is time in days, alpha is the asymptote or maximum germination, m is the growth rate, and gamma is a parameter controlling the inflection point. These parameters were estimated using nonlinear least squares regression.

For germination analysis, final germination percentage at 35 days was calculated, along with two germination speed indices: time to reach 25% germination (T25) and mean germination time (MGT) [27]. T25 was used instead of T50, as most treatments did not reach 50% cumulative germination within the 35-day evaluation. Final germination percentage and MGT were compared using one-way ANOVA, after verifying assumptions of normality and homoscedasticity. Pairwise comparisons among treatments were conducted using Tukey's test.

All analyses were performed using R software version 4.4.1 [28], with the packages "growthmodels" (for nonlinear regression), "binom" (for binomial confidence intervals), and "multcompView" (for mean comparison visualizations).

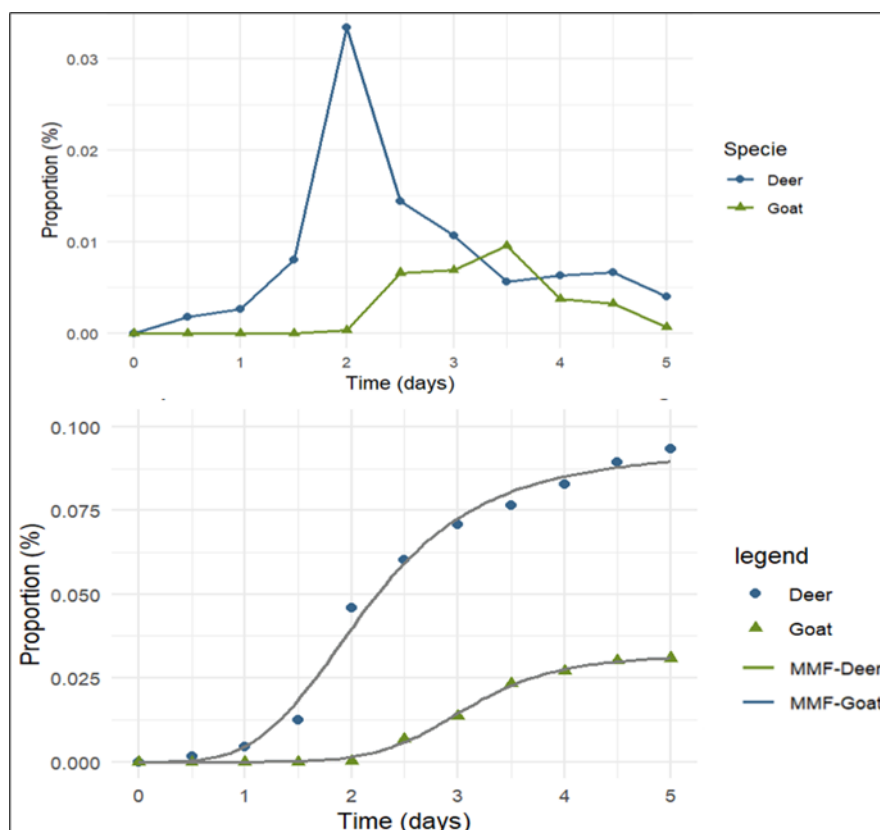
## 3. Results

### 3.1. Seed Recovery

The estimated number of seeds consumed was 2,214 for goats and 1,914 for white-tailed deer (WTD), derived from the quantity of fruits ingested by the animals during the experimental trials. The recovery of *N. pallida* seeds from dung was 68 seeds (3.09%) for goats and 178 seeds (9.36%) for deer. Table 2 presents the estimated parameters of the Morgan-Mercer-Flodin model for seed recovery; the asymptotes correspond to the final percentages of recovered seeds. Maximum seed recovery in WTD occurred at 48 hours (2 days), with 35.7% of total recovered seeds being defecated by that time. In goats, the peak recovery occurred at 84 hours (3.5 days), with 31% of seeds recovered (Figure 2).

**Table 2.** Model parameters for recovered *N. pallida* seeds from dung according MMF function.

Specie	Model parameters			Final recovery
	alpha	gamma	m	
White-tailed deer	0.093	19.320	3.847	0.093
Goat	0.032	2949.000	7.094	0.031

**Figure 2.** Proportion of *N. pallida* seeds recovered from white-tailed deer (WTD) and goat feces. The curves show the predictions of the Morgan-Mercer-Flodin (MMF) model.

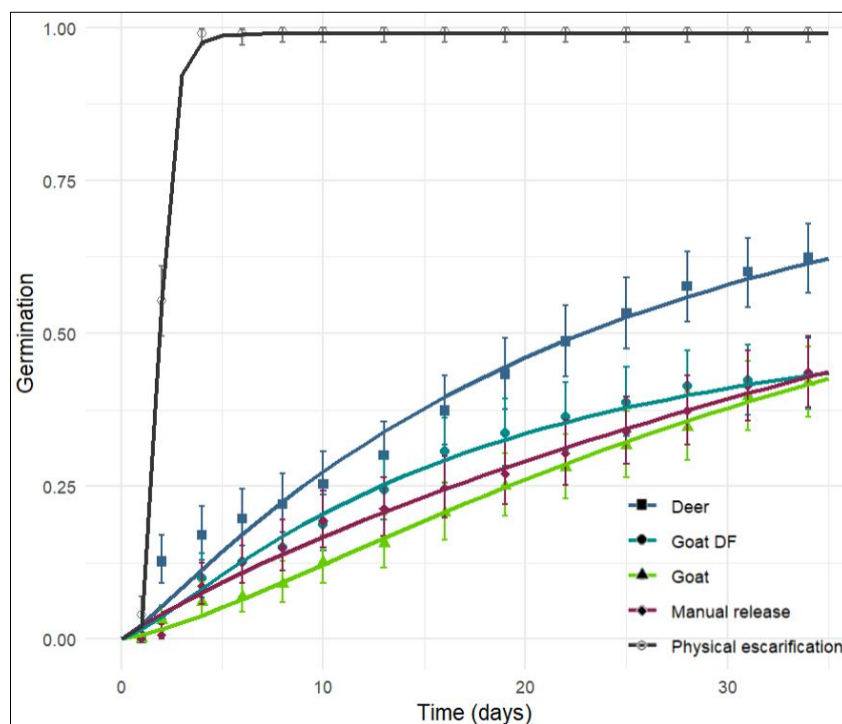
### 3.2. Germination Dynamics

The modeled curves revealed substantial differences in the cumulative germination dynamics among treatments (Figure 3). The highest asymptotic values (alpha) were observed for the manual extraction treatment (171%), followed by deer (101%), physical scarification (99%), confined goats (96%), and goats under dry forest grazing conditions (63%).

**Table 3.** Model parameters for predicting the proportion of germinated seeds of *N. pallida* according to the Morgan-Mercer-Flodin.

Treatment	alpha	gamma	m	R2	Final germination (35 days)	Final germination (90 days)
Manual release	1.71	76.66	0.92	0.87	0.46	0.76
Physical scarification	0.99	0.45	0.59	0.99	0.99	0.99
Goat	0.96	157.26	1.36	0.90	0.44	0.71
Deer (WDT)	1.01	39.76	1.17	0.91	0.63	0.82
Goat in dry forest	0.61	37.72	1.28	0.87	0.44	0.56

Alpha represents the asymptotic of the model (maximum germination). Final germination is shown at 35 and 90 days.



**Figure 3.** Germination dynamics of seeds from *Neltuma pallida* for different treatments. Error bars indicate the Clopper-Pearson binomial confidence interval, and the curves show predictions according to the Morgan-Mercer-Flodin Models.

Final germination was significantly higher in seeds subjected to physical scarification and in seeds recovered from white-tailed deer dung ( $F = 40.99$ , Tukey test,  $p < 0.001$ ). In contrast, seed passage through the gastrointestinal tract of goats, both under confined conditions and in dry forest grazing, had no significant effect compared to manually extracted seeds. Except for the physical scarification treatment, all treatments exhibited mean germination time (MGT) values similar to the untreated control (manual extraction). However, significant differences were detected between the confined goat and grazing goat treatments ( $F = 40.96$ , Tukey test,  $p < 0.001$ ). The time to reach 25% germination (T25) was lowest in physically scarified seeds (1.59 days), followed by seeds recovered from deer dung (8.98 days). Grazing goats reduced T25 to 12.81 days, whereas confined goats increased it to 19.25 days (Table 4).

**Table 4.** Effect of different treatments on seed germination of *Neltuma pallida*.

Treatment	Germination (%)		T25 (MMF-models)	MGT (days)	
	mean $\pm$ SE	Group		mean $\pm$ SE	Group
Manual release	45.00 $\pm$ 4.28	a	16.24	15.74 $\pm$ 1.58	ab
Deer (WTD)	62.67 $\pm$ 2.76	c	8.98	14.09 $\pm$ 0.91	ab
Goat	43.00 $\pm$ 3.00	a	19.25	17.64 $\pm$ 0.88	a
Goat in Dry Forest	43.67 $\pm$ 2.39	a	12.81	12.97 $\pm$ 0.58	b
Physical scarification	99.33 $\pm$ 0.42	b	1.59	2.48 $\pm$ 0.03	c

Means with a letter in common are not significantly different (Tukey test,  $P < 0.05$ ), T25 values estimated from the Morgan models.

## 4. Discussion

### 4.1. Seed Recovery

Overall, seed recovery from goat and white-tailed deer (WTD) dung was low (9.4 % and 3.09 % respectively), consistent with previous studies. Recovery rates below 11% have been reported for

Fabaceae species ingested by goat in dry forests of Brazil [29]. In Mediterranean shrublands, seed recovery from goat dung ranges from 1% to 31% [30,31]. These values also fall within the range reported for other *Neltuma* species. For *N. juliflora*, recovery rates of 7% in goat and 15% in cattle have been reported [15]; for *N. glandulosa*, 9.2% and 11.3% for goats and sheep, respectively [32]; and for *N. pallida*, 2.1% in camels [18]. These results confirm that a large proportion of seeds are lost during mastication and rumination processes. Regarding seed retention time, it was shorter in WTD (peak at 48 hours) than in goats (peak at 84 hours), which aligns with previous reports for medium-sized seeds, typically retained between 72 and 96 hours [29]. For shrub species, the majority of seeds consumed by goats are excreted between 24 and 48 hours [31]. The shorter retention time of *N. pallida* seeds in WTD can be explained by a relatively smaller stomach size, fewer subdivisions, and larger openings that facilitate the passage of ingested material [24]. "Similarly, a shorter seed recovery time in goats compared to cows has been reported for *N. juliflora* [15] and *N. flexuosa* [33]. This variation in seed retention is attributed to the presence of structures and mechanisms that delay the passage of ingested material in different types of ruminants: WTD (concentrate selector) exhibit shorter retention than goats (intermediate feeders), which in turn have shorter retention than cows (grazers) described by [24].

#### 4.2. Seed Germination Dynamics

Species of the genus *Neltuma*, like many members of the Fabaceae family, exhibit physical dormancy. The seed coat contains a water-impermeable layer that prevents imbibition and germination [16]. This impermeability is due to a palisade layer of tightly packed cells impregnated with water-repellent substances [16,34]. This type of dormancy can be broken through mechanical or acid scarification [35]. The 99% germination observed in the physical scarification (sandpaper) treatment, compared to the much lower germination in manually extracted seeds, confirms the presence of physical dormancy in *N. pallida*.

Similar results have been reported for *N. juliflora* using chemical scarification (Alvarez et al., 2017). Among the biological scarification treatments, only white-tailed deer (WTD) significantly increased the final germination of *N. pallida* seeds. These findings are consistent with prior evidence indicating that physical dormancy is not always broken through endozoochory [36]. The differences observed between WTD and goats under experimental feeding conditions may be explained by variation in hydrochloric acid (HCL) concentration in the abomasum. WTD have a greater proportion of HCL-producing tissues in the abomasum compared to goats, an adaptation related to their distinct evolutionary feeding strategies [24]. However, the duration of seed exposure to acidic conditions is also important, as it can influence the extent of scarification by HCL [35].

In terms of germination speed (T25), seeds recovered from goat dung (both experimental feeding and dry forest grazing) showed variable responses compared to untreated seeds (manual extraction). T25 was reduced in seed from goats under experimental feeding conditions. These differences may be linked to the frequency of seed consumption. In the experimental setup, goats ingested seed only once, while in the forest, goats consumed *Neltuma* fruits daily. Previous studies have shown that variable exposure time of physically dormant seeds to HCL can influence germination timing, particularly T50 [35]. Therefore, seeds recovered from grazing goat may have originated from fruits ingested at different times and retained for variable durations. Daily ingestion could also alter the overall passage time of seeds through the gastrointestinal tract. In similar studies with shrub species in Spain, seed germination following goat digestion showed inconsistent effects, with longer retention times not always improving germination outcomes [30,37].

## 5. Conclusions

Our study found clear differences in the recovery and germination of *N. pallida* seeds ingested by goats. These results align with known morphophysiological differences among ruminant feeding types (Hofmann, 1989). Biological scarification by white-tailed deer was more effective than that by goats in enhancing seed germination. Additionally, the frequency of fruit ingestion by goats may

either increase or reduce the germination speed of *N. pallida* seeds recovered from dung. Although both species contribute to seed dispersal, the current low population density of white-tailed deer means that goats are now the primary seed dispersers in these dry forests. While goat digestion does not significantly enhance final germination rates, it does play a key role in seed release and dispersal. Moreover, ingestion and subsequent encapsulation of seeds in dung can protect them from bruchid predation [25]. Goat dung also provides a favorable microenvironment by offering nutrients and moisture that can support seedling establishment, as observed in *N. juliflora*. [13].

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