

# Tree-climbing goats disperse seeds during rumination

Most people are familiar with domestic goats (*Capra hircus*) climbing on rocks, but few know they are talented tree climbers too. In temperate countries where green pastures abound, goats do not need to climb trees to forage, but in arid regions the only available forage is sometimes found on the tops of evergreen shrubs and trees. Furthermore, goats often like seasonal fruits and collect them directly from fruiting trees when fallen fruits have been depleted. In southwestern Morocco, where the average annual rainfall is only 300 mm, goats climb the endemic argan tree (*Argania spinosa*; Figure 1). Herders assist kid goats in learning to climb and even occasionally prune the trees to facilitate climbing. During the autumn, when herbaceous vegetation is lacking, goats devote 74% of their foraging time to “treetop grazing” (El Aich *et al.* 2007) (Figure 2). We previously observed Spanish and Mexican goats grazing on short trees or shrubs, but in Morocco we were astonished to see between 10 and 20 goats regularly climbing thorny 8–10-m-tall argan trees, mostly defoliated after intensive grazing. The purpose of our research was to verify that goats regurgitated the nuts of argan fruits while ruminating, as we postulated that this could be a potential dispersal mechanism for large seeds.

Argan forests are ecologically and economically important in southern Morocco, which is a developing country. The forests serve as an effective barrier for the Saharan Desert and provide local people with wood, fodder for livestock, cooking oil, medicine, and cosmetic materials. Since the 1990s, argan oil has emerged as a luxury commodity in international markets (Lybbert *et al.* 2011). To extract the oily kernels, the fleshy pulp of the tree fruits

must first be removed and the hard nuts broken manually. Most popular accounts (and some scientific papers; eg Charrouf and Guillaume 2008) say that to remove the pulp, traditional Berbers feed the fruit to goats so the nuts pass through the digestive system and the seeds can be collected from the manure. However, goats do not usually defecate large seeds, so we were skeptical about the possibility that they could defecate nuts of about 22 mm in length and 15 mm in width, on average. Instead, we wondered whether goats, which are ruminants, might spit out the nuts while chewing their cud, as we had seen goats do when fed with olive (*Olea europaea*) and dwarf palm (*Chamaerops humilis*) fruits in Spain (unpublished data). Moroccan goat herders confirmed that goats regurgitated most argan nuts while ruminating, although regurgitations and excrement found on the ground are usually mixed, resulting in misunderstandings about the way the nuts were expelled.

Why is it important that goats regurgitate and spit out seeds from the cud? For plants there are well-known reproductive benefits associated with dispersing their seeds far from the maternal parent, including a greater probability of seed and seedling survival. To successfully disperse, many plant species produce edible fruits that attract frugivorous vertebrates, which ingest the fruits and transport the seeds inside their body until they are released elsewhere by regurgitation or defecation. This dispersal mechanism is called endozoochory. Many investigations have focused on endozoochory by ruminants, but most of them neglect the potentially important role of seeds spat from the cud. For example, a review on seed dispersal by

domestic and wild ungulates associates endozoochory exclusively with seeds contained in dung samples (Albert *et al.* 2015). The possibility of ruminant ungulates spitting out some viable seeds from the cud is not even mentioned in this and other comprehensive reviews. However, a few studies – predominantly conducted in tropical areas – have described seed regurgitation during rumination, stating that a “less well-reported form of endozoochory is specific to ruminants. Large viable seeds are spat out after some time in the rumen” (Feer 1995). Janzen (1985) explained that white-tailed deer (*Odocoileus virginianus*) “regurgitate the nuts (of *Spondias mombin*) while chewing their cud” and that “nuts never pass into the lower digestive tract”. Here, we report on this largely overlooked form of endozoochory



**Figure 1.** Goats grazing on an argan tree in southwestern Morocco. In the fruiting season, many clean argan nuts are spat out by the goats while chewing their cud.

by domestic goats, and suggest that this could be widespread in other domestic and wild ruminants.

To illustrate the potential of domestic ruminants to spit viable seeds from their cud, we supplied Spanish domestic goats with fruits differing in size and structure, corresponding to five species (six varieties) of plants, including five drupes or pomes (fleshy fruits) and one legume (pods): *Chamaerops humilis* (Arecaceae; 16.3 × 11.0 mm average seed dimensions), *Crataegus monogyna* (Rosaceae; 6.1 × 4.8 mm), *Celtis australis* (Ulmaceae; 6.7 × 6.3 mm), *Olea europaea* var *sylvestris* (Oleaceae; 10.2 × 5.4 mm), *O. europaea* var *domestica* (Oleaceae; 13.3 × 5.8 mm), and *Ceratonia siliqua* (Fabaceae; 7.5 × 5.3 mm). For all the plant species, we recovered appreciable numbers of seeds that the goats had regurgitated, despite not being able to find all of the seeds, since the goats were not subject to controlled conditions. As might be expected, larger seeds were more frequently spat out during rumination (minimum 30–45% of the ingested seeds for *C. humilis* and *O. europaea* var *domestica*, versus less than 10% for the other species). Our observations suggest that almost any seed could be ejected during mastication, spat from the cud, digested, or defecated. We tested the viability of regurgitated seeds by incubating them in a solution containing tetrazolium chloride; the embryo and endosperm of most seeds (71.5%) were stained red, indicating they were viable after processing by goats (Hartmann and Kester 1983). In southern Spain we have observed sheep, captive red deer (*Cervus elaphus*), and fallow deer (*Dama dama*) also spitting out seeds during rumination, and Yamashita (1997) described parrots in Brazil collecting clean palm seeds in places where cows had gathered and ruminated during the night, but did not consider the implications for seed dispersal.

If spitting viable seeds from the cud is widespread among ruminants, as we suggest, its ecological relevance could be important. According to Hackmann and Spain (2010), wild ruminants (weighing from 2 to 800 kg) number about 75 million and have native populations on all continents except Australia and Antarctica, whereas domestic ruminants (40–800 kg) number 3.6 billion and are found everywhere. Most wild ruminants include fruits and leaves in their diet, as do goats (sometimes climbing on trees to forage) and, to a lesser extent, other domestic ruminants. Though a fraction of domestic ruminants live permanently in fenced enclosures (and are therefore unable to disperse seeds into the field), the free-ranging ones plus their wild counterparts are certainly able to mobilize large quantities of viable seeds. Besides, because seeds remain in the rumen for hours or days, they may potentially be



**Figure 2.** In some arid habitats, such as argan forests, most green vegetation is on the tops of trees and goats climb there to feed.

released very far from the mother plants. This is especially true for domestic ruminants driven hundreds of kilometers in search of productive pastures (transhumance; eg Manzano and Malo 2006) and also for wild ruminants making seasonal migrations (eg Berger 2004).

In conclusion, many previous studies that investigated the role of ruminants as seed dispersers were based exclusively on dung analyses and may have underestimated an important fraction of the total number of dispersed seeds. Moreover, this fraction of seeds should correspond to plant species with particular fruit and seed traits (eg large linear dimensions) differing from those of plant species dispersed exclusively or mostly through defecation. Importantly, the seeds of some species are unlikely to survive passage through the ruminant lower digestive tract so that spitting from the cud may represent their only, or at least their main, dispersal mechanism. It is therefore essential to investigate the effectiveness of this overlooked mechanism of seed dispersal in various habitats and systems.

#### ■ Supporting Information

References and additional web-only material may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/fee.1488/suppinfo>

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