

Beyond Endozoochory: New World Oropendolas Also Disperse Large Seeds via Stomatochory

José L. Tella ^{1,*} , Cristina B. Sánchez-Prieto ² , Pedro Romero-Vidal ¹ , Guillermo Blanco ³ 
and Fernando Hiraldo ¹ 

¹ Department of Conservation Biology and Global Change, Estación Biológica de Doñana (EBD-CSIC), 41092 Sevilla, Spain; pedro.romero@ebd.csic.es (P.R.-V.); hiraldo@ebd.csic.es (F.H.)

² Department of Zoology, University of Granada, 18071 Granada, Spain; cris@ugr.es

³ Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales CSIC, 28006 Madrid, Spain; g.blanco@csic.es

* Correspondence: tella@ebd.csic.es

Abstract

Identifying seed dispersal mechanisms is key to understanding plant responses to global change and, ultimately, ecosystem resilience. New World Oropendolas (Icteridae) are widespread frugivorous birds traditionally regarded as seed dispersers through endozoochory, acting as gulpers by swallowing whole fruits and as mashers when biting into large fruits with pulp, and later defecating viable seeds. Here, we provide photographic evidence that Crested Oropendolas (*Psarocolius decumanus*) also disperse whole fruits through stomatochory by transporting them in their bills. We observed individuals removing fruits from oil palms (*Elaeis guineensis*), carrying them in flight, and subsequently consuming the pulp while holding the fruit against branches with their feet. Previously, we also observed Montezuma Oropendolas (*Psarocolius montezuma*) carrying fruits of three plant species in flight. In all cases, the plants produced large fruits and seeds whose dispersal by endozoochory would be constrained by their size. These observations reveal a previously overlooked dispersal mechanism in a widespread group of Neotropical frugivores and suggest that the role of Oropendolas in seed dispersal may be broader than previously recognized.

Keywords: frugivores; oil palm tree; *Psarocolius*; seed dispersal; zoochory



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Seed dispersal is a fundamental ecological process underpinning the maintenance of plant communities, biodiversity, and ecosystem functioning. Identifying the mechanisms by which seeds are dispersed is therefore essential for understanding the capacity of plant populations, and ultimately ecosystem resilience, to respond to the multiple drivers of global change. It has been estimated that at least half of the world's plant species rely on animals for seed dispersal [1]. Among these, frugivores are traditionally regarded as the primary seed dispersers because they consume fleshy fruits and disperse viable seeds after passage through the digestive tract (i.e., endozoochory). Their role is particularly important in tropical ecosystems, where nearly 90% of woody plant species are thought to depend on frugivores for seed dispersal [2–4].

However, animal-mediated seed dispersal encompasses a broader diversity of mechanisms that have received comparatively less attention. A recent synthesis of seed dispersal interactions across Europe challenged long-standing assumptions about dispersal syndromes, showing that endozoochory by frugivores represents only a subset of animal-mediated seed dispersal and that dispersal syndromes based solely on fruit morphology

substantially underestimate the diversity of plant–animal interactions [5]. Alternative dispersal mechanisms, including epizoochory (seed transport via attachment to the body surface of animals) and stomatochory (seed transport in the beak or mouth), may play a much greater role in ecosystems dominated by different plant communities or disperser assemblages [6,7]. Consequently, researchers have called for greater attention to overlooked disperser guilds, dispersal mechanisms, and plant functional groups to bridge major knowledge gaps, improve predictions of ecosystem responses to global change, and develop more effective conservation strategies [8–10].

Here, we present photographic evidence of a previously undescribed seed dispersal mechanism in New World Oropendolas (Icteridae). Oropendolas (genus *Psarocolius*) are medium- to large-sized passerines (length 35–45 cm, body mass 124–330 g [11]) that inhabit tropical forests throughout Central and South America [12]. Their large gape [11] enables them to swallow fruits whole, and they are therefore widely regarded as classic “gulper” frugivores when swallowing whole fruits, as well as “mashers” when biting into large fruits with pulp to consume them, and they disperse seeds via endozoochory [11,13–15]. Our observations, however, reveal that oropendolas can also disperse large fruits and seeds externally by carrying them in the bill (i.e., stomatochory).

On 27 December 2025, we observed birds feeding on fresh fruit bunches of an oil palm (*Elaeis guineensis*) in Lajas Medio, Panama, between 07:16 and 08:53 h. A flock of Orange-chinned Parakeets (*Brotogeris jugularis*) fed on the oily mesocarp of the large, ovoid fruits (2.5–5 cm long). During the observation period, solitary Crested Oropendolas (*Psarocolius decumanus*) visited the fruit bunch on three occasions. On each visit, an individual detached a fruit with its bill and carried it away in flight (Figure 1).



Figure 1. Crested Oropendola (*Psarocolius decumanus*) after plucking an oil palm fruit, just before taking flight with the fruit in its bill (Photo: José L. Tella).

On the first two occasions, the birds disappeared into the forest within a few metres of the palm, preventing us from determining either the transport distance or the subsequent handling of the fruit. On the third occasion, however, an individual flew with the fruit

to a perch at the forest edge, approximately 10 m from the palm, where it manipulated the fruit. The Oropendola held the fruit against the branch with one foot while removing the fleshy mesocarp with its bill in a manner resembling that of parrots (Figure 2). Before consuming all the pulp, it picked up the partially defleshed fruit with its bill and flew into the forest, disappearing from view approximately 40 m from the perch. As reported for several parrots and macaws feeding on palm fruits, which consume the pulp while leaving the seeds intact [16], this behavior allows birds to act as fruit mashers while transporting undamaged seeds via stomatochory, potentially resulting in effective seed dispersal when seeds are dropped far from the mother plant.



Figure 2. The same Crested Oropendola shown in Figure 1 holding the fruit with its foot while removing the pulp with its bill (Photo: José L. Tella).

These well-documented observations complement earlier opportunistic records obtained in Costa Rica during a nationwide survey of parrots conducted in 2018, where we observed Montezuma Oropendolas (*Psarocolius montezuma*) transporting the fruits of three plant species by stomatochory (Table 1), suggesting that this behaviour is not restricted to a single species or locality. On one occasion, we observed a Montezuma Oropendola flying with a fruit of the Coral Tree (*Erythrina fusca*) held in its bill. These fruits are woody pods approximately 20 cm long, each containing 3–15 seeds. The bird was already carrying the fruit when first detected and flew approximately 340 m before disappearing from view, as estimated with the laser rangefinder integrated into our binoculars. Consequently, the actual seed dispersal distance was likely considerably greater.

Table 1. Observations of plants dispersed by Montezuma Oropendolas (*Psarocolius montezuma*) through stomatochory in Costa Rica, showing the range sizes (in cm) of their fruits and seeds.

LOCALITY	DATE	PLANT SPECIES	FAMILY	NATIVE	FRUIT LENGTH	FRUIT WIDTH	SEED LENGTH	SEED WIDTH
Westfalia	22 April 2018	<i>Nephelium lappaceum</i>	Sapindaceae	No	3–7	3–5	2.5–4	1–1.5
Guápiles	24 April 2018	<i>Erythrina fusca</i>	Fabaceae (Papilionoideae)	Yes	14–33	1.4–1.8	1.2–1.8	0.5–0.8
Tortuguero	24 April 2018	<i>Inga spectabilis</i>	Fabaceae (Mimosoideae)	Yes	60–100	2–3	4	2.5

On another occasion, we observed a flock of 16 Montezuma Oropendolas feeding on ripe Rambutan (*Nephelium lappaceum*) fruits. At different times, two individuals removed fruits from the tree, carried them in their bills to the same perch approximately 38 m away, and then flew into the forest while still carrying the fruits, disappearing from view.

On a third occasion, seed dispersal by Montezuma Oropendolas was facilitated by the foraging activity of White-crowned Parrots (*Pionus senilis*). A flock of 12 parrots was using their powerful bills to open the large pods of Guaba Machete (*Inga spectabilis*) and fed on the sweet, cotton-like aril surrounding the seeds. Three Montezuma Oropendolas approached the feeding parrots, and two displaced them from the pods. The oropendolas then inserted their bills into the openings created by the parrots, extracted seeds enclosed in the aril, and flew into the forest carrying them in their bills. They disappeared from view at distances of 42 and 53 m, respectively.

Taken together, our observations of Crested and Montezuma Oropendolas, although limited in number, document the long-distance dispersal of large fruits and seeds from both native and exotic plants through stomatochory (Table 1).

A recent review suggests that stomatochory may play a more important role in seed dispersal than previously recognized, allowing animals to transport fruits and seeds that are too large to be swallowed and dispersed through endozoochory [7]. The apparent concentration of stomatochory in a relatively small number of taxonomic groups—including bats, squirrels and Old World monkeys among mammals, and parrots and corvids among birds—may reflect a research bias rather than a true ecological pattern, with the behaviour remaining overlooked in other taxa due to limited research [7]. Moreover, the combination of multiple dispersal modes, particularly endozoochory and stomatochory within the same bird species, may be more widespread than previously thought [17]. This appears to be the case for Oropendolas, frugivores widely recognized as seed dispersers through endozoochory [11], but which, as we show here, can also disperse seeds through stomatochory by transporting fruits and intact seeds in their bills after consuming the pulp. Importantly, Crested and Montezuma Oropendolas, like other animals that practice stomatochory [7,16], are capable of transporting large fruits and seeds, including those of so-called megafaunal plants, whose dispersal is thought to have been substantially disrupted by the extinction of large-bodied mammal frugivores [18]. These observations suggest that the role of Oropendolas in seed dispersal may have been underestimated and deserves further investigation.

According to the size-matching hypothesis [19], fruit–frugivore interactions are constrained by morphological matching between fruit traits and frugivore morphology, which in turn determines the ability of frugivores to access, handle, and process fruits of different sizes and shapes [20–22]. Oropendolas may transport fruits that are smaller than their gape width via stomatochory, facilitating efficient pulp removal while avoiding the energetic costs associated with swallowing and subsequently regurgitating large, bulky seeds. Nevertheless, despite their relatively large gape widths (16.2 and 19.3 mm in Crested

and Montezuma Oropendolas, respectively [11]), several of the fruits we observed these birds carrying in their bills were unlikely to have been swallowed whole, suggesting that stomatochory may provide an alternative means of processing fruits that exceed their capacity for ingestion. As documented in parrots [23], the combination of these dual feeding strategies—gulping and mashing—with the use of both endozoochory and stomatochory substantially broadens the range of seed sizes that oropendolas can disperse and the distances over which they can transport them. While tiny seeds embedded in the pulp are typically dispersed over relatively long distances through endozoochory, this functional versatility also allows for alternative combinations of seed size, dispersal mode, and dispersal distance. For example, small seeds extracted together with the pulp may be transported over short distances via stomatochory, whereas large seeds contained in multi-seeded fruits may be dispersed over variable distances through either endozoochory or stomatochory. With 11 species distributed across much of the tropical forests of Central and South America [12], Oropendolas may represent a widespread and previously overlooked component of seed dispersal networks.

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