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Frugivory and seed dispersal by the invasive knight anole (*Anolis equestris*) in Florida, USA

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ABSTRACT

Introduced species can have diverse effects on recipient ecosystems. Here we share observations suggesting the formation of a reciprocally positive interaction, seed dispersal, between an introduced lizard and a native palm. We present evidence that the large arboreal lizard (*Anolis equestris*), native to the West Indies but well-established in south Florida USA, has a diet dominated by the fruit of several native trees including the endangered royal palm (*Roystonea regia*). We also show that seeds passed through the gut of *A. equestris* are viable, suggesting their role as seed dispersers in their introduced range. These findings are the first to document the passage of viable seeds by *Anolis* lizards, a speciose and ecologically-diverse Neotropical group that exhibits widespread frugivory. We believe these observations highlight potentially important, but understudied interactions between these Neotropical lizards and plants.

Human-assisted movement of flora and fauna has resulted in the establishment of many species in areas outside of their native distributions. Many introductions have led to dramatic population declines and extinctions of native species mediated by negative trophic interactions such as predation (Blackburn et al., 2004). Non-native species can also cause harm by disrupting positive interspecific interactions such as pollination and seed dispersal (Rogers et al., 2017; Traveset and Richardson, 2006, 2014) or by aiding the establishment of other non-native species (Simberloff, 2006; Simberloff and Holle, 1999). However, biological invasions can also result in the formation of positive ecological interactions between native and non-native species that benefit native species through the initiation, amendment, or reinforcement of positive ecological interactions (e.g., Garcia et al., 2014; Pemberton and Liu, 2008; Schlaepfer et al., 2011; Traveset et al., 2013). Here, we present preliminary evidence for a mutualistic relationship, seed dispersal, between a rare, native tree and an introduced omnivorous lizard, the knight anole (*Anolis equestris*). First, we review diet data for this invasive lizard in south Florida and then argue that they are an ecologically-important seed disperser in their native and invasive ranges.

Knight anoles (*A. equestris*) are medium-sized, arboreal lizards native to Cuba (Fig. 1). Following human-aided establishment in Florida during the mid-20th century, *A. equestris* has spread throughout south Florida (Camposano et al., 2008). Introduced *A. equestris* are found in a variety of habits, have large home ranges for a lizard (~0.06 ha; Nicholson and Richards, 2011), and exist at moderate population densities (18–30 ind/ha; Dalrymple, 1980). And like most anoles, *A. equestris* is omnivorous, consuming a wide variety of animal and plant material (Giery et al., 2013; Herrel et al., 2004; Kartzinel and Pringle, 2015; Schoener, 1968; Stroud et al., 2017). However, available information on *A. equestris* diet show that these large anoles regularly consume fruit, especially palms and figs, suggesting the potential for ecologically relevant positive interactions with plants, for example, seed dispersal.

To assess the potential for *A. equestris* to act as effective seed dispersers we examined their diet, and the viability of ingested and passed seeds. We first examined the dissected stomach contents of ten adult *A. equestris* caught at Fairchild Tropical Botanic Garden in Miami, Florida, USA between August 2015 and August 2016. Second, to determine the potential for knight anoles to pass viable seeds we collected and planted two *R. regia* seeds after they passed through the digestive tract of an *A. equestris* briefly held in captivity. We planted these seeds in a single pot in a climate-controlled greenhouse on July 20th 2016 at Florida International University.

The results of our brief study showed that, as with other studies, fruit was frequently consumed as were invertebrates such as snails.

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Fig. 1. Knight anoles (*Anolis equestris*) are large, arboreal, and highly frugivorous lizards native to Cuba and introduced to Miami, Florida in the mid-20th century. This adult female was found perched in a strangler fig (*Ficus aurea*) in Miami, Florida.
Photo by S. Giery.

Table 1
Knight anole (*Anolis equestris*) diet summaries (number of individuals assessed, 'n', are included below each study reference). Data presented in columns are the proportion of individual knight anoles with prey taxa in their stomach, *P*(*n*). For this study we also present the proportion of total stomach contents by volume, *P*(*vol*) following Magnusson et al. (2003).

	Brach, 1976 $n = 10$	Dalrymple, 1980 $n = 18$	Giery et al., 2013 $n = 24$	This study $n = 10$	
Taxa	*P*(*n*)	*P*(*n*)	*P*(*n*)	*P*(*n*)	*P*(*vol*)
Coleoptera	0.1	0.7	0.5		
Homoptera		0.6			
Hymenoptera	0.2	0.6	0.3	0.1	0.01
Orthoptera	0.1	0.4	0.2		
Lepidoptera	0.1	0.2	0.3	0.2	0.26
Hemiptera		0.1			
Diptera		0.2			
Arachnida	0.4	0.4	0.1		
Gastropoda		0.2	0.1	0.3	0.43
Vertebrata		0.1		0.1	< 0.01
Fruit	0.5	0.3	0.5	0.6	0.24

Pooled frequencies from recovered stomach contents included Royal palm fruit (*R. regia* $n = 13$), terrestrial snails (*Liguus fasciatus*; $n = 1$, *Zachrysia* sp.; $n = 5$), small unidentified seeds ($n = 6$), lepidopteran larvae ($n = 2$), a honey bee (*Apis mellifera*; $n = 1$), and a small section of lizard tail (*Anolis carolinensis*; $n = 1$; Table 1). All identifiable plant remains observed in stomach contents were the seeds and fleshy fruit of *R. regia* (the integrity of the hard seeds did not appear compromised). In addition, our seed germination trials showed that seeds passed by *A. equestris* are viable. Of the two *R. regia* seeds we planted, one successfully germinated after 60 days. This seedling was 8 cm tall 130 days later (growth rate = 0.04 cm/day) and continued to appear healthy (Fig. 2). At 190 days we excavated the second seed which had recently germinated and also appeared healthy (Fig. 2).

We believe our results highlight three important aspects of *A. equestris* ecology. First, *A. equestris* are highly frugivorous. Second, seeds passed through the *A. equestris* digestive tract are viable. Third, routine consumption of *R. regia* fruits and their viability post-consumption, suggests this interaction may be important for *R. regia.* We briefly discuss these points below.

Anecdotal reports of vertebrate prey such as birds, frogs, and other lizards (geckos and anoles) are common for *A. equestris* (Barbour and Ramsden, 1919; Collette, 1961; Ljustina and Stroud, 2016; Nicholson and Richards, 2011; Ruibal, 1964; Stroud, 2013). Yet, these observations generally disagree with taxonomically detailed and quantitative assessments of *A. equestris* diet that clearly illustrate a diet dominated by invertebrates (e.g., butterflies, snails) and fruits, especially figs and palm fruits (Brach, 1976; Dalrymple, 1980; Giery et al., 2013; Table 1). Indeed, only two of the 62 *A. equestris* examined across multiple studies contained vertebrate prey (Table 1), a low frequency comparable to that observed in other anole species (Giery et al., 2013; Stroud et al., 2017).

Frugivores often affect the viability of seeds they consume. While ingestion often positively influences germination rates, effects are variable and species-specific (Traveset, 1998). Reptiles have received relatively little research in this regard, yet data show reptiles have variable effects on the viability of seeds they ingest (Burgos-Rodriguez et al., 2016; Rosenblatt et al., 2014; Strong and Fragoso, 2006; Traveset et al., 2016). While we lack data necessary to evaluate the viability of other ingested species of seed, or even whether the effect of ingestion is positive for *R. regia*, we do show that ingestion by an *Anolis* lizard is not necessarily negative. Additionally, Broschat and Donselman (1988) showed that *R. regia* germination rates increase substantially (from 18 to 52%) following simulated frugivory (deinhibition - removal of fleshy pericarp from the seed). In conjunction, these data suggest that ingestion by *A. equestris* has a positive effect on germination rate, however, more data on seed fates are required to evaluate this hypothesis.

Roystonea regia is a large (up to 30 m), ecologically and economically important palm native to the West Indies (Cuba, The Bahamas), the western Caribbean (Mexico, Honduras, Belize), and Florida, USA (Zona, 1991, 1996). Despite its large distribution, high economic importance, and large (~ 1 cm diameter), colorful fruits, a detailed understanding of *R. regia* seed dispersal is lacking, especially outside of Cuba. Within Cuba, arboreal birds and several bat species routinely ingest and disperse *R. regia* seeds - a typical animal-mediated (endozoochory) dispersal mode in palms (Zona, 1996; Zona and Henderson, 1989). Additionally, several researchers have noted an association between *R. regia* and *A. equestris* in Cuba (Barbour and Ramsden, 1919; Collette, 1961), but a role for *A. equestris* as a seed disperser was never mentioned. However, within Florida little is published about the seed dispersal community associated with *R. regia*. Indeed, most of the avian

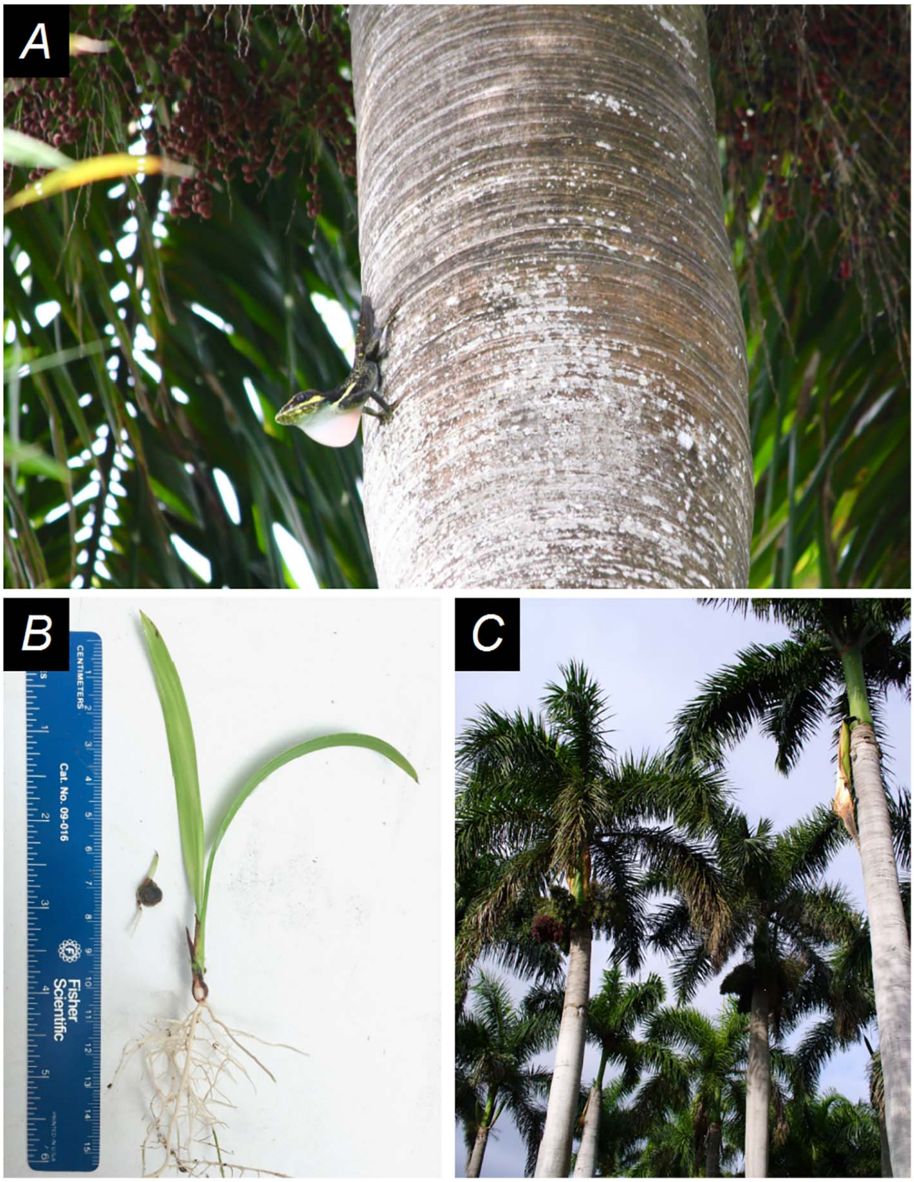

Fig. 2. Adult knight anoles (*Anolis equestris*) often inhabit the crowns of royal palms (*Roystonea regia*) in Florida and Cuba. Note the numerous ripe fruits above this displaying male photographed at our study site in Coral Gables, Florida (A). *Roystonea regia* seedlings resulting from seeds passed naturally by a wild-caught *A. equestris*. Both seeds were planted at the same time, but germinated nearly 130 days apart (B). Adult royal palms can reach 30 m high and are an ecologically and economically important plant throughout their range (C).
Photos by J. Stroud (A & B) and S. Zona (C).

and bat dispersers known from Cuba are absent from Florida suggesting a depauperate mutualist community there. Yet, in combination with published diet data, the original observations we report here clearly suggest the potential for lizard mediated seed dispersal in Florida, and probably Cuba. Establishing this interaction may be especially important for the conservation success of peripheral *R. regia* populations in Florida where they are State Endangered.

More generally, positive ecological interactions such as seed dispersal are fundamental for maintaining tropical plant diversity (Howe and Smallwood, 1982). In carrying seeds away from the parent plant, animals can ameliorate density/distance dependent mortality helping to increase local diversity (Janzen, 1970; Schupp et al., 2010). Seed dispersal research, however, often focusses on birds and mammals, while seed dispersal in other taxonomic groups such as lizards has consistently been overlooked, or considered an island novelty (Olesen and Valido, 2003). However, recent literature has suggested that frugivory is more widespread in lizards than previously recognized, and may represent a fundamentally important ecological interaction for a wide range of plant taxa (Godinez-Alvarez, 2004; Nogales et al., 2017; Rodriguez-Perez and Traveset, 2010; Valido and Olesen, 2007). For example, to our knowledge this is the first published evidence of successful seed germination following frugivory by anoles – an ecologically diverse genus with ca. 400 species distributed throughout the Neotropics (Losos, 2009). Although anoles are largely invertivores, frugivory is frequently recorded in larger species (Herrel et al., 2004; Pough, 1973). Yet, the broader ecological importance of frugivory (e.g., seed dispersal) in anoles has not been investigated, despite being an important model system for decades.

We believe our observations raise several important points. First, considerable attention has been focused on the effects of species introductions on the stability and function of plant-animal mutualisms (Traveset and Richardson, 2014). While disruptions to existing mutualisms due to species invasions appear widespread (Traveset and Richardson, 2006), species invasion can also form new, ecologically valuable linkages with native species. Second, our findings underscore the important ecological insights gained through taxonomically detailed and quantitative examination of diet rather than collation of anecdotal accounts (e.g., see Winemiller, 1989; Winemiller et al., 2001). Finally, while our observations of seed dispersal in *Anolis* lizards are new, they seem representative of a widespread ecological phenomenon. But despite its apparent ubiquity lizard-mediated seed dispersal continues to evade detailed ecological study despite excellent insights from recent studies in the Galapagos islands (Nogales et al., 2017; Traveset et al., 2013, 2016), and Europe (Godinez-Alvarez, 2004;

Olesen and Valido, 2003; Valido and Olesen, 2007; Wotton et al., 2016). We believe our findings, in combination with other efforts (e.g., Burgos-Rodriguez et al., 2016; Iverson, 1985), highlight the need for additional assessment of the effectiveness of lizards as seed dispersers in the Greater Caribbean and elsewhere.

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