



The effect of frugivorous birds on seed dispersal and germination of the invasive Brazilian pepper tree (*Schinus terebinthifolius*) and Indian laurel (*Litsea glutinosa*)



P. Dlamini^a, C. Zachariades^{a,b}, C.T. Downs^{a,*}

^a Centre for Invasion Biology, School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, Private Bag X01, Scottsville 3209, South Africa

^b Plant Protection Research Institute, Agricultural Research Council, Private Bag X6006, Hilton 3245, South Africa

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ABSTRACT

Biological invasions are a major threat to biodiversity in most parts of the world. The success of invasive fleshy fruiting plants is linked to the role of native avian frugivores. By ingesting and excreting/regurgitating viable seeds, avian frugivores are able to promote germination and disperse the seeds of these invasive fleshy fruiting plants. The Brazilian pepper tree (*Schinus terebinthifolius*) and the Indian laurel (*Litsea glutinosa*) are both invasive species in South Africa, particularly in KwaZulu-Natal. We examined the effect of native birds (Cape white-eyes (*Zosterops virens*), red-winged starlings (*Onychognathus morio*), speckled mousebirds (*Colius striatus*) and dark-capped bulbuls (*Pycnonotus tricolor*) on germination and dispersal of *S. terebinthifolius* and *L. glutinosa* seeds by comparing them to those of whole and manually de-pulped *S. terebinthifolius* and *L. glutinosa* fruit. By comparing the seed retention times and fruit consumed by the various avian species, we examined which avian species were likely to have the most effect on germination and dispersal of *S. terebinthifolius* and *L. glutinosa*. We found that all avian species readily consumed the fruit of *S. terebinthifolius* and that (through pulp removal by gut passage) these avian species played a vital role in the germination time and success of *S. terebinthifolius*. Most of the avian species consumed *L. glutinosa* fruit (though not as much as *S. terebinthifolius*), with speckled mousebirds being the only exception. However, ingestion of *L. glutinosa* fruit had no positive effect on germination as none of the seeds germinated (including the control seeds). Variances in body mass and bill size could potentially mean that larger birds play a greater role in seed dispersal as they ingested a greater number of seeds. Further studies need to be conducted on *L. glutinosa* in order to determine the conditions in which it germinates in the field and how these may be replicated for germination experiments in the laboratory.

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1. Introduction

The second biggest threat to biodiversity worldwide (after direct habitat destruction) is biological invasions (Richardson and van Wilgen, 2004). Invasive alien plants (IAPs) are non-native, naturalized plant species that have successfully spread outside of their native range (Richardson et al., 2000b). IAPs are a concern as they compete with native species and disrupt the functioning of natural ecosystems which can further result in biodiversity and economic losses (Ehrenfeld, 2003; Hejda et al., 2009; Vilà et al., 2011). The success of IAPs in foreign ranges can be generally attributed to their rapid growth, early reproduction, abundant seed production and fleshy fruits (which are often associated with bird-dispersal) (D'Avila et al., 2010).

Understanding the mechanisms and pathways by which invasive plant species establish themselves in foreign countries is vital as such information can be used in their eradication or management, and aid potential biological control efforts (D'Avila et al., 2010). Frugivorous vertebrates (particularly birds) often play a major role in the seed dispersal of invasive plants, especially as the passage of seeds through their gut sometimes increases germination and seeds are dispersed further from the parent plant. IAPs may compete with native plant species for the attention of dispersal agents (Bass, 1990; Lafleur et al., 2007). This may result in preferences for invasive plants, stemming from the formation of loose mutualisms with native dispersers (particularly birds and mammals) (Richardson et al., 2000a). Alternatively, IAPs may increase native seed dispersal or could have no effect (Wilson and Downs, 2012). It is such mutualisms that lead to the successful spread and establishment of fleshy-fruited alien plants (Fraser, 1990; Chimera and Drake, 2010). Fruit traits (such as morphology and nutritional composition) that are associated with avian frugivory play an

* Corresponding author.

E-mail addresses: zachariades@arc.agric.za (C. Zachariades), downs@ukzn.ac.za (C.T. Downs).

important role in developing preferences (Gosper and Vivian-Smith, 2009).

Small, single-seeded fleshy fruits tend to have more frugivore visitors than larger multi-seeded fruit (Gosper and Vivian-Smith, 2009). Seed retention time also influences potential seed dispersal distance (Meisenburg and Fox, 2002) and when predicting plant movement patterns and range expansion processes, long-distance seed dispersal is an important factor to consider (Jordaan et al., 2011). The process of seed dispersal by frugivorous birds (and frugivores in general) involves the ingestion of fruit pulp and the defecation (or regurgitation) of intact, viable seeds (Meisenburg and Fox, 2002; Buckley et al., 2006). Once consumed, seeds may undergo both chemical and mechanical digestion (McKey, 1975; Barnea et al., 1991), thus affecting both the percentage of seeds that germinate and the rate of germination (D'Avila et al., 2010). Seed coat abrasion and pulp removal are the principal means by which germination rates may be affected by frugivory (Meisenburg and Fox, 2002). The degree of seed coat abrasion may also be influenced by the retention time of seeds in the gut (Sorensen, 1984; Murray et al., 1994). However, some studies show that the seed germination of invasive alien plants is rapid irrespective of avian digestion or not (Barnea et al., 1990, 1991; Jordaan et al., 2011).

The Brazilian pepper tree (*Schinus terebinthifolius* Raddi (Anacardiaceae)) is native to subtropical South America and was introduced into South Africa for ornamental, hedging, and shade/shelter purposes (Panetta and McKee, 1997). Here it is classified as a Category 1b invasive under the National Environmental Management: Biodiversity Act (NEMBA) in the Eastern Cape, KwaZulu-Natal, Limpopo and Mpumalanga Provinces, and Category 3b in Free State, Gauteng, North-West, Northern Cape and Western Cape Provinces. It is highly adaptive and so can take the form of either an evergreen shrub (2–3 m) or a tree (up to 15 m) (Lenzi and Orth, 2004a). It produces small, cream-white, dioecious (male and female) flowers that appear from September to March. A single *S. terebinthifolius* tree can produce a large number of bright red (when ripe) drupe-like fruits of a 3–5 mm diameter, surrounding a single internal seed. Due to its high tolerance of extreme moisture conditions, shaded environments and saline conditions, and its allelopathic effects on surrounding plants, *S. terebinthifolius* may compete with native species (D'Avila et al., 2010). *Schinus terebinthifolius* is an aggressive pioneer species, rapidly growing during its seedling and sapling stages, particularly in nutrient-depleted soils (de Souza et al., 2001). It also rapidly occupies early and secondary stages, mainly resulting from a high dispersal of seeds (Backes and Irgang, 2002). Like so many other damaging invasive plants, it is generally dispersed by native frugivores (Meisenburg and Fox, 2002). In its native Brazil, it is pollinated by an array of different flies, wasps and bees and its fruiting period is from January to October (in South Africa fruit normally sets in winter months) (Lenzi and Orth, 2004b; Jesus and Monteiro de Araujo Filho, 2013). In South Africa there has been some evidence of *S. terebinthifolius* being dispersed by frugivorous birds (pers. obs.).

Indian laurel, *Litsea glutinosa* (Lour.) C.B. Rob. (Lauraceae) is an invasive species in South Africa (NEMBA Category 1b) that is especially problematic in KwaZulu-Natal Province, particularly in the vicinity of Durban. It has a native range extending from the Himalayas, through South-East Asia to Oceania (Heuzé et al., 2015), and was introduced into South Africa for cultivation (Ross, 1972). It is an evergreen shrub or tree (6–10 m), producing small, yellow-orange flowers that appear from October to May (summer) and with lance-shaped leaves. The fruits are pea-sized shiny black berries with a single seed inside (Jacq et al., 2005).

We determined whether native avian frugivores ingest the fruits of *S. terebinthifolius* and *L. glutinosa* and whether the ingestion of the seeds of these two species by various frugivorous avian species has an effect on their potential dispersal, and germination time and success. We hypothesized that the time and percentage of germination of *S. terebinthifolius* and *L. glutinosa* seeds would be affected by ingestion (gut passage) by native avian species. We tested this by comparing

the germination time and percentage of seeds that were ingested by the avian species compared with whole-fruit and fruit that had their pulp manually removed. The potential effect of frugivory on dispersal was assessed by comparing the seed retention times and fruit consumed by the various avian species.

2. Methods

2.1. Maintenance of study birds

With ethical clearance from the University of KwaZulu-Natal Ethics Committee and permits from Ezemvelo KZN Wildlife (Ethics 020/15/animal; EKZNV OP 485/2016), we caught and housed four indigenous bird species. Eleven Cape white-eyes (*Zosterops virens*), four red-winged starlings (*Onychognathus morio*), six speckled mousebirds (*Colius striatus*) and six dark-capped bulbuls (*Pycnonotus tricolor*) were caught in the Pietermaritzburg area (29°37'32"S 30°24'5"E) using mist nets.

Before experiments began, birds were housed separately (according to species) in outside aviaries (1 × 2.12 × 2.66 m) at the Animal House Unit, University of KwaZulu-Natal, Pietermaritzburg campus. They were fed a daily maintenance diet comprised of a mix of minced exotic fruits (apples, pears, bananas) and supplements of AviPlus Softbill/Mynah pellets and crumble (Avi-products, Durban, South Africa). Water was available ad libitum. After about 3–5 days, feeding trials commenced, subject to the availability of invasive fruit.

2.2. Bird species

The avian species used for this study were selected based on field observations in which bird species were observed feeding on the invasive plants in question (*S. terebinthifolius* and *L. glutinosa*). These birds are also quite common in suburban areas in and around Durban and Pietermaritzburg, KwaZulu-Natal Province. The Cape white-eye is a small (~9 g) passerine bird, native to southern Africa (Smith and Bowie, 2005). Although Cape white-eyes' diet mainly consists of invertebrates (especially aphids), they also feed on nectar and fruit (Downs, 2008). The red-winged starling has a native range from Ethiopia to the Cape in South Africa (Craig, 2005). They feed on a variety of seeds, nectar and berries and weigh between 115 and 155 g (Craig, 2005; Craig and Feare, 2010). The speckled mousebird is native to South Africa, weighs ~50 g and feeds on leaves, flowers and fruits (Downs et al., 2000; Dean, 2005). The dark-capped bulbul weighs ~40 g, occurs in South Africa, and feeds on fruits, insects, flower buds and nectar (Lloyd, 2005).

2.3. Feeding trials

Individual birds were placed in cages in a constant environment room set at 25 °C, on a 10 L:14D (light, dark) cycle and were acclimatized for 5 days. For two days before the experimental day, the birds were fed with the daily maintenance diet combined with the experimental fruit (*S. terebinthifolius* during the first trial and *L. glutinosa* during the second trial). A single feeding trial, for the purposes of this experiment, was defined as a 10 h period (from 07 h00 to 17 h00) in which the birds were exposed to (and fed on) the experimental (invasive) fruit. A single trial was conducted for each invasive plant and each individual bird in a species constituted a single replicate (e.g. six dark-capped bulbuls made six replicates for that species). *Schinus terebinthifolius* and *L. glutinosa* fruits were collected from the Durban area. The respective fresh fruit was weighed twice daily on trial days (at 07 h00, before the trial, and 17 h00, after) to determine the amount of fruit consumed by each bird. The birds were also individually weighed 30 min before and after each trial. Control fruits were placed in the experimental room and weighed before and after each trial to determine their evaporative water loss. Excreta were collected from the

cages of each bird at the end of each trial. The maintenance diet was fed to birds in-between trials ad libitum.

2.4. Seed retention time

Seed retention or transit time was measured in order to determine the effect on potential seed dispersal distance of *S. terebinthifolius* and *L. glutinosa* fruits. It was measured as the time from when the individual birds first started feeding on the respective fruit in each trial to the time when the first undigested seeds appeared in their excreta. For regurgitated seeds, the seed retention time was measured as the time from when birds first fed to the time when undamaged seeds appeared in regurgitated food. Seed retention time was measured on feeding trial days only.

2.5. Germination trials

Schinus terebinthifolius and *L. glutinosa* seeds from each individual bird's excreta or regurgitation were collected and planted. Due to the extremely high number of *S. terebinthifolius* seeds found in the excreta of each avian species, only 200 seeds were planted from each bird species in total. Seeds were planted (1 cm deep) in trays containing potting soil (with no additives), no more than 24 h after feeding. Manually de-pulped and whole-fruit seeds of *S. terebinthifolius* and *L. glutinosa* were planted concurrently as controls, in the same manner as ingested seeds. All trays were placed in a shade house (in which temperature was set at a min of 15 °C and max of 25 °C), and watered and monitored daily. When seedlings emerged through the soil surface, this was considered as germination. Once counted, each seedling was then removed from the tray in order to avoid recounting. The time taken for seeds to germinate was also recorded. Germination trials began when seeds were planted and ended once all seedlings had emerged. All of the germination trials started in the winter, as this is when both plants set fruit (pers. obs.). *Schinus terebinthifolius* trials ran from July to August and *L. glutinosa* trials ran from July to September. In the case of non-germination trials were cut off after 82 days. Rabena (2010) found clay loam soil to be the most suitable for *L. glutinosa* germination, however, to allow for comparison we used a standard potting soil with no additives.

2.6. Data analysis

Germination for each avian species individual was expressed as: germination time—the number of days it took for seeds to first emerge; and germination success—the percentage and cumulative percentage of seeds that germinated from the total number of planted seeds. The germination-related characteristics of each avian species individual were represented as follows: seed retention time—the time between ingestion and expulsion (excreta or regurgitation); total fruit consumed—weight of fruit consumed (expressed in g and then per g body mass); and germination potential—the potential effect that each bird species may have on the number of germinated seeds based on germination percentage and total number of excreted seeds (mean no. of excreted seeds ÷ 100 * mean germination %).

Data for fruit consumed (g and g/g body mass), retention time (min), germination time (days), germination success (percentage, not cumulative) and germination potential (potential no. of germinated seeds) were compared among bird species using One-way ANOVA tests in STATISTICA (Statsoft, Tulsa, version 7, USA). As most of the variables had non-normally distributed data, the data was log-transformed in order to obtain normality. The data for germination time of *S. terebinthifolius* as well as seed retention time and fruit consumption for *L. glutinosa* were not transformed as they were normally distributed.

3. Results

3.1. Fruit consumed

All avian species readily consumed *S. terebinthifolius* fruit, although the total amount of *S. terebinthifolius* fruit consumed by the various bird species was significantly different from one another (ANOVA, $F_{3, 22} = 9.805$, $p < 0.001$, Fig. 1a). The amount of fruit consumed by red-winged starlings was significantly higher than that of dark-capped bulbuls (24 ± 2.2 g; $p < 0.001$), speckled mousebirds (31 ± 2.4 g) and Cape white-eyes (17 ± 1.7 g; $p < 0.001$). Speckled mousebirds also ingested a significantly higher amount of *S. terebinthifolius* fruit than Cape white-eyes ($p < 0.001$). Dark-capped bulbuls and Cape white-eyes did not differ significantly in the amount of *S. terebinthifolius* fruit they consumed ($p = 0.062$).

The amount of *S. terebinthifolius* fruit consumed per gram of body mass by each avian species also varied significantly from one another (ANOVA, $F_{3, 22} = 20.324$, $p < 0.001$, Fig. 1c). Cape white-eyes had the highest fruit consumption per gram body mass (1.5 ± 0.09) as it was significantly higher than that of dark-capped bulbuls (0.6 ± 0.12 ; $p < 0.001$), red-winged starlings (0.4 ± 0.15 ; $p < 0.001$) and speckled mousebirds (0.6 ± 0.13 ; $p < 0.001$).

The avian species consumed less *L. glutinosa* fruit than *S. terebinthifolius*, but there was a significant variation in the total amount of this fruit consumed per day between avian species (ANOVA, $F_{2, 16} = 20.885$, $p < 0.001$, Fig. 1b). Red-winged starlings consumed a significantly higher amount of *L. glutinosa* fruit (18 ± 0.7 g) than dark-capped bulbuls (8 ± 2.1 g; $p = 0.001$), and Cape white-eyes (6 ± 1.0 g; $p < 0.001$). Speckled mousebirds did not consume any *L. glutinosa* fruit at all.

There was also some variation in the amount of *L. glutinosa* fruit consumed per gram of body mass by each avian species (ANOVA, $F_{2, 16} = 4.647$, $p = 0.026$, Fig. 1d). Cape white-eyes consumed a higher amount of fruit per gram body mass (0.52 ± 0.080) than the red-winged starlings (0.13 ± 0.132 ; $p = 0.026$). The amount of fruit consumed per gram body mass by the dark-capped bulbuls did not vary significantly from that of the other avian species.

3.2. Retention time

The time that *S. terebinthifolius* seeds were retained in the digestive system before passing out in the excreta varied significantly among the avian species (ANOVA, $F_{3, 22} = 4.997$, $p = 0.009$, Fig. 2a). The dark-capped bulbuls had a significantly lower seed retention time (mean \pm SE, 13 ± 3.0 min) than both the speckled mousebirds (25 ± 3.2 min; $p = 0.010$), and the Cape white-eyes (22 ± 2.2 min; $p = 0.019$). Speckled mousebirds and Cape white-eyes did not differ significantly in their retention times and both had the highest retention times. The retention time of red-winged starlings (16.5 ± 3.61 min) did not differ significantly from that of any of the other avian species.

There were no significant differences in the seed retention times of the avian species that consumed *L. glutinosa* fruit (ANOVA, $F_{1, 6} = 1.186$, $p = 0.3180$, Fig. 2b). Dark-capped bulbuls had a seed retention time of 40 ± 9.1 min while red-winged starlings 52 ± 9.1 min. Cape white-eyes did not consume the entire fruit, but rather pecked at it, only ingesting the fruit pulp, and thus had no seed retention time. As mentioned speckled mousebirds did not consume any *L. glutinosa* fruit so had no effect on retention time.

3.3. Germination time

The mean time it took for *S. terebinthifolius* seedlings to first emerge did not vary greatly among bird species as only red-winged starlings and speckled mousebirds showed a significant difference (ca. 15 and 20 days respectively, $p = 0.045$, Fig. 3). There was, however, a significant difference between the germination time of the whole fruit

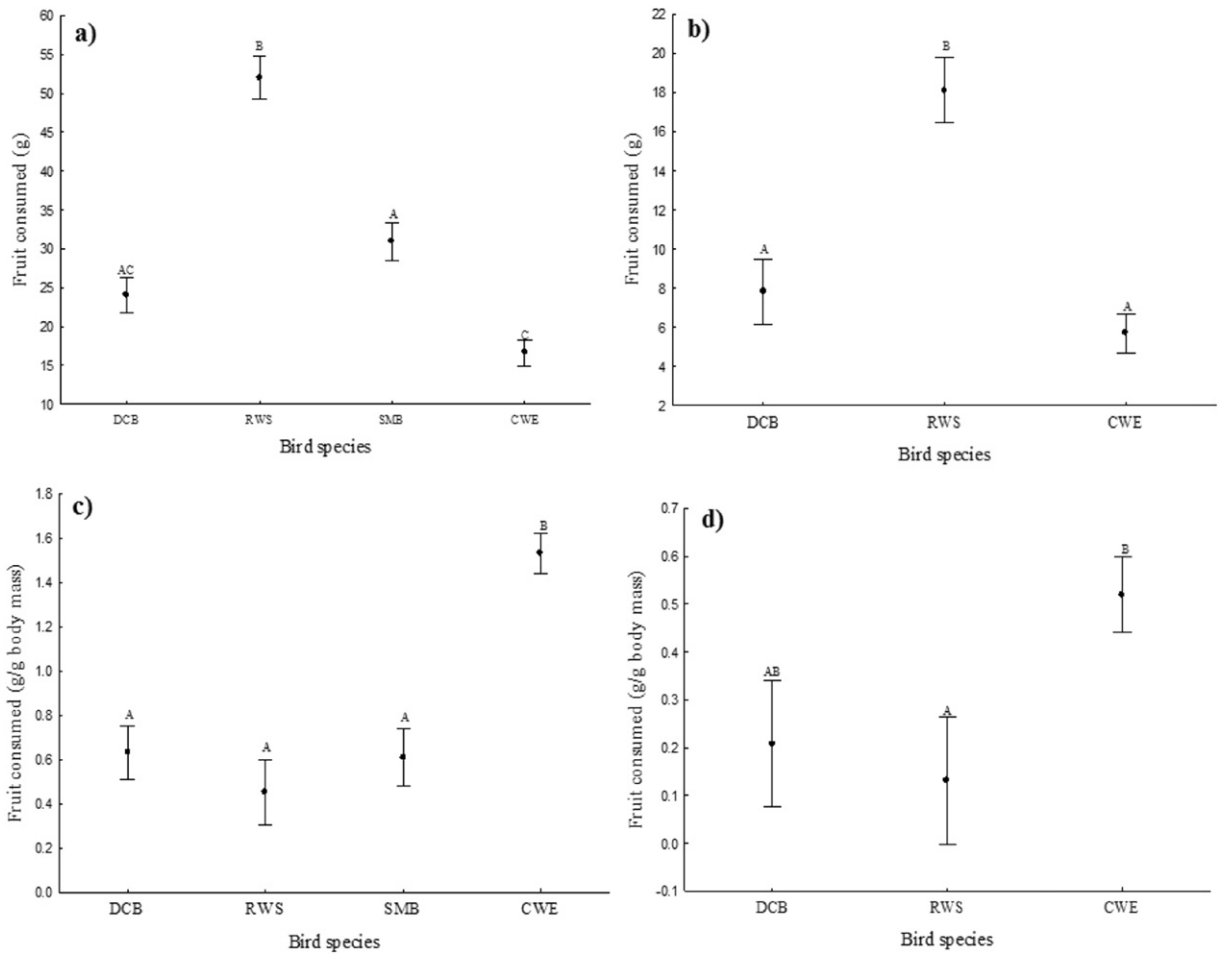


Fig. 1. Fruit consumed (in grams (a, b) and per gram body mass (c, d)) by dark-capped bulbuls (DCB), red-winged starlings (RWS), speckled mousebirds (SMB) and Cape white-eyes (CWE) that were fed fruit of *S. terebinthifolius* (a and c) and *L. glutinosa* (b and d). (Black circles are means; vertical bars denote \pm standard error. Means that do not share common letters between/among them were significantly different (Tukey's HSD, $p < 0.05$)).

compared with all the bird-ingested seeds, as well as when compared to the manually de-pulped seeds as the whole fruit germinated at a significantly slower time (ANOVA, $F_{5, 28} = 9.805$, $p < 0.001$, Fig. 3). The whole

fruit had a mean germination/emergence time of 25 days which was significantly higher than that of seeds ingested by dark-capped bulbuls (ca. 18 days; $p < 0.001$), red-winged starlings (ca. 15 days; $p < 0.001$),

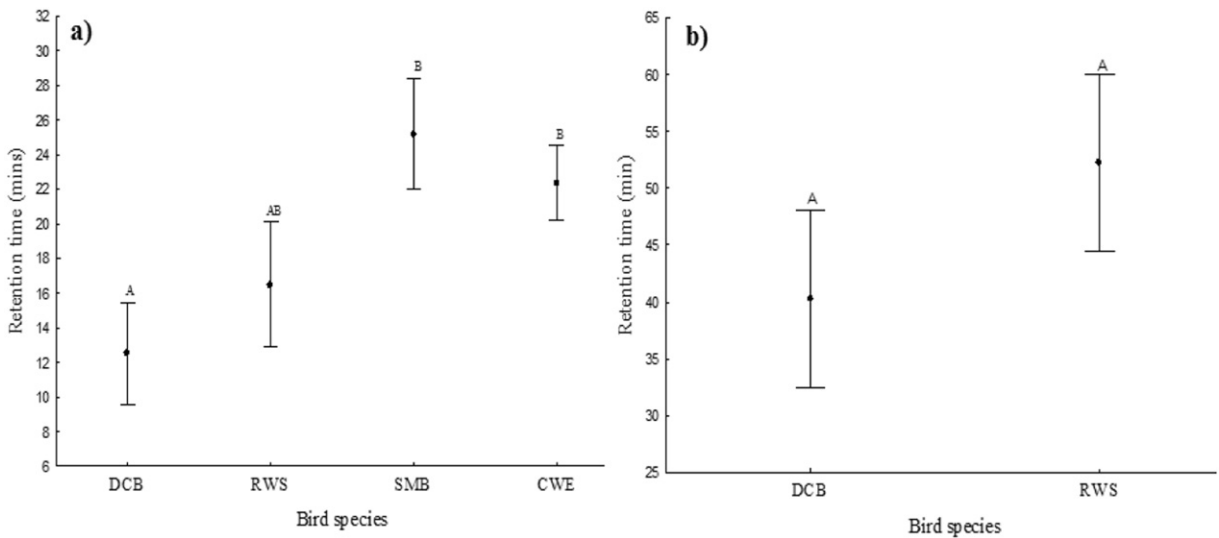


Fig. 2. Seed retention time dark-capped bulbuls (DCB), red-winged starlings (RWS), speckled mousebirds (SMB) and Cape white-eyes (CWE) fed the fruit of a) *S. terebinthifolius* and b) *L. glutinosa*. (Solid black circles are means, vertical bars denote \pm standard error. Means that do not share common letters between/among them were significantly different (Tukey's HSD, $p < 0.05$)).

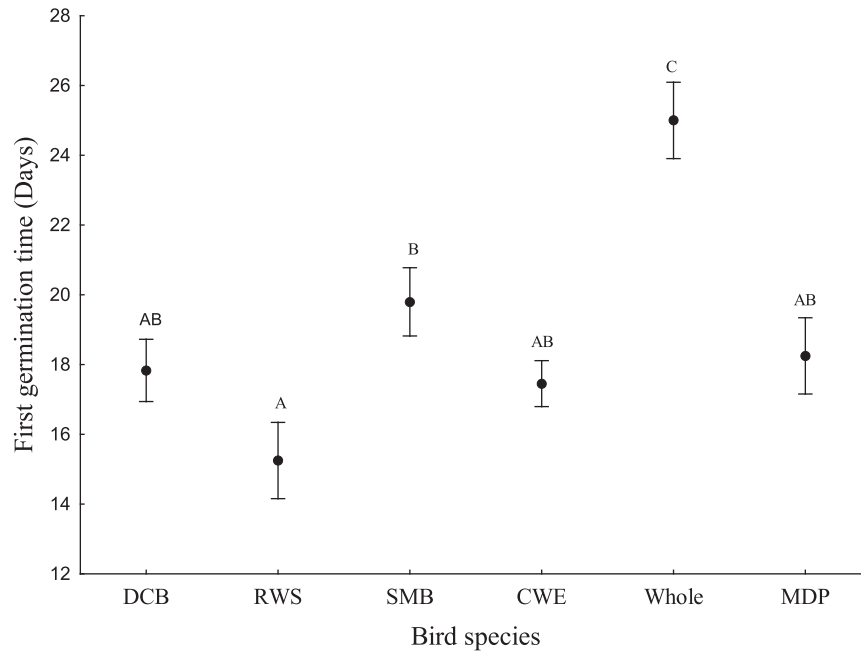


Fig. 3. First germination time (days) of *S. terebinthifolius* seeds ingested by dark-capped bulbuls (DCB), red-winged starlings (RWS), speckled mousebirds (SMB) and Cape white-eyes (CWE) as well as whole and manually de-pulped fruit. (Solid black circles are means, vertical bars denote \pm standard error. Means that do not share common letters between/among them were significantly different (Tukey's HSD, $p < 0.05$)).

speckled mousebirds (ca. 20 days; $p = 0.016$), Cape white-eyes (ca. 18 days; $p < 0.001$) as well as manually de-pulped seeds (ca. 18 days, $F = 4.781$, $df = 28$, $p = 0.002$). None of the *L. glutinosa* seeds (whole fruit, depulped or ingested seeds) germinated despite monitoring for an extensive period (82 days).

3.4. Germination success

The overall percentage (not cumulative) of germinated *S. terebinthifolius* seeds did not vary among bird species. There

was, however, a significant difference between the germination percentages of the whole fruit when compared with the respective bird-ingested seeds (ANOVA, $F_{5, 28} = 10.915$, $p < 0.001$). This pattern is represented in Fig. 4 which shows cumulative data. The whole fruit had a mean germination percentage of 23% which was significantly lower than that of seeds ingested by dark-capped bulbuls (45%, $F = 0.01134$, $df = 28$, $p = 0.0016$), red-winged starlings (48%; $p = 0.001$), speckled mousebirds (46%; $p = 0.002$), Cape white-eyes (58%; $p < 0.001$) as well as manually de-pulped seeds (65%; $p < 0.001$).

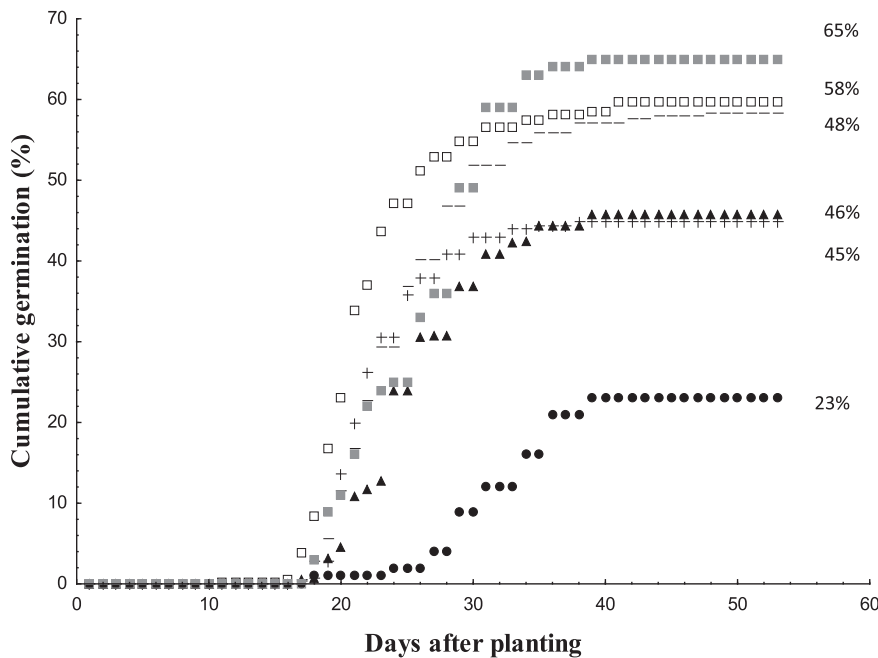


Fig. 4. Cumulative germination percentage of *S. terebinthifolius* seeds ingested by dark-capped bulbuls (+), red-winged starlings (---), speckled-mousebirds (▲), Cape white-eyes (□) as well as whole (●) and manually de-pulped fruit (■).

3.5. Germination potential

The mean potential number of germinated *S. terebinthifolius* seeds varied among avian species (ANOVA, $F_{3, 22} = 16.507$, $p < 0.001$, Table 1). Red-winged starlings had a significantly higher germination potential for *S. terebinthifolius* than the other avian species: dark-capped bulbuls ($p = 0.003$), speckled mousebirds ($p = 0.002$) and Cape white-eyes ($p = 0.033$). The second highest germination potential was for both dark-capped bulbuls and speckled mousebirds, with no significant difference between these two species. Cape white-eyes had the lowest germination potential for *S. terebinthifolius* and this was significantly lower than both red-winged starlings ($p < 0.001$), and dark-capped bulbuls ($p = 0.03$).

4. Discussion

4.1. Fruit consumed

The amount of *S. terebinthifolius* fruit consumed by various avian species is an important variable to consider as it is directly related to the number of seeds ingested and passed out by each species. Red-winged starlings (the largest of the avian species) consumed the most fruit, followed by speckled mousebirds, dark-capped bulbuls and Cape white-eyes (the smallest avian species consumed the least fruit). The number of seeds excreted by each avian species followed a similar pattern to that of fruit consumed.

The amount of *L. glutinosa* fruit consumed by each avian species is not necessarily related to the number of seeds excreted/regurgitated as smaller avian species (i.e. Cape white-eye) did not consume the entire fruit, but rather just pecked at the fruit pericarp or pulp, so did not act as legitimate seed dispersers. Although in some cases smaller birds can act as seed dispersers of larger fruit if they are able to carry the fruit away from the plant or if the fruit contains multiple small seeds (Rey et al., 1997), this was not the case with *L. glutinosa* and Cape white-eyes. The relatively large size of *L. glutinosa* (~8 mm in diameter) (Jacq et al., 2005) makes it impossible for a bird with a small gape size, such as small as the Cape white-eye, to consume it whole and unlikely that the bird would be able to carry the fruit away. There was, however, a correlation in the amount of fruit consumed and seeds excreted/regurgitated for red-winged starlings and dark-capped bulbuls. Once again the largest avian, the red-winged starlings, consumed the most of these fruit and dark-capped bulbuls and Cape-white eyes consumed similar amounts. The speckled mousebirds did not consume any *L. glutinosa* fruit.

4.2. Retention time

Studies conducted on the effect of seed retention time on germination success have been contradictory. While some have reported long retention times to have a positive effect (Barnea et al., 1991), others found it to have a negative effect (Murray et al., 1994; Charalambidou et al., 2003), and some have found no effect at all (Barnea et al., 1990, 1991). In our study, retention time did not have an effect on germination success of *S. terebinthifolius* seeds as all the seeds that were ingested by avian species had similar germination success despite their differences in retention times. Speckled mousebirds and Cape white-eyes

had the longest retention times, followed by red-winged starlings and lastly dark-capped bulbuls. The lack of variation in germination success despite the variations in avian seed retention times showed that as an invasive, *S. terebinthifolius* germinates well irrespective of avian disperser ingestion as found by Jordaan et al. (2011). With regard to the avian species used in our study, longer retention times may potentially play more of a role in promoting dispersal than they do in further increasing germination success as in other invasives (Meisenburg and Fox, 2002; Jordaan et al., 2011). Given that all the avian species used in this study fly more than 0.5 km from a fruiting tree (pers. obs.), it is likely that *S. terebinthifolius* seeds may be dispersed over relatively long distances, particularly given the retention time of its seeds.

Dark-capped bulbuls and red-winged starlings had similar retention times for *L. glutinosa* fruit, both of which had no effect on germination as none of the *L. glutinosa* fruit germinated (including the control treatments).

4.3. Germination time

The time it takes for seeds to germinate has been shown to be affected by pulp removal in previous studies (Yagihashi et al., 1999). Our study showed a similar trend as whole fruit of *S. terebinthifolius* germinated at a slower rate than seeds that had been ingested by all of the avian species (dark-capped bulbuls, red-winged starlings, speckled mousebirds and Cape white-eyes). The acceleration in germination time of seeds ingested by avian species is a result of pulp removal when fruit pass through the gut; this is made more evident by the fact that seeds that were manually de-pulped had a similar germination time to those that were ingested by birds. There was also a slight variation in germination time among the avian species as seeds ingested by red-winged starlings generally germinated faster than those ingested by speckled mousebirds. However, for the most part, *S. terebinthifolius* seeds that were ingested by the avian species used in this study germinated at a similar rate.

As mentioned above, none of the *L. glutinosa* fruit germinated (including the control treatments). Though it is unclear why this is, it may be (at least partially) due to seed predation by rodents after the seeds had been planted as the germination trials were conducted in a shade house that could possibly be accessed by rodents. We placed rodent live traps in the shade house to catch any possible rodent predators, however we were unsuccessful in catching any, and so we were unable to confirm if rodents were seed predators. Attempts to germinate seed elsewhere have met with mixed success, with low germination at times (Ratree, 2006; Rabena, 2010; C. Zachariades, pers. obs.) however in the field, many seedlings are sometimes found (C. Zachariades, pers. obs.). It is possible that larger native avian frugivores, such as hornbills, disperse the seeds of *L. glutinosa* as found in Thailand (Ratree, 2006).

4.4. Germination success

Previous studies (Barnea et al., 1991; Panetta and McKee, 1997; Meyer and Witmer, 1998; Jordaan et al., 2011; Voigt et al., 2011) have found the manual removal of fruit pulp and that which is caused by avian gut passage to have a similar effect on germination success. A similar pattern was observed in this study as the germination success

Table 1
Potential number of germinated *S. terebinthifolius* seeds based on mean number of seeds excreted and germination percentage.

	Mean no. of seeds excreted per day	No. of seeds planted	Mean germination success (%)	Mean potential no. of germinated seeds
Red-winged starlings (n = 4)	995.5	200	48	489
Speckled mousebirds (n = 6)	407.2	200	46	185
Dark-capped bulbuls (n = 6)	468	200	45	215
Cape white-eyes (n = 11)	220.5	200	58	129

(percentage) of *S. terebinthifolius* was similar to that of seeds ingested by avian species. The ingestion of *S. terebinthifolius* seeds by avian species had a positive effect on germination success. Because this positive effect on germination success was similar to that of manually de-pulped seeds, it is evident that the effect is due to pulp removal, rather than seed coat abrasion. All of the avian species used in our study, namely dark-capped bulbuls, red-winged starlings, speckled mousebirds and Cape white-eyes, had similar effects on the percentage of seeds that germinated. This may be an indication of similar morphological traits of the avian species' digestive tracts, at least in regards to pulp removal (Barnea et al., 1991; Traveset and Willson, 1997; Yagihashi et al., 1999).

4.5. Germination potential

The number of seeds excreted, as well as the germination percentage of seeds excreted by each avian species, can be used to estimate the number of seeds for which each bird species can potentially promote germination. Unsurprisingly, red-winged starlings (which consumed the most fruit) had the highest potential germination for *S. terebinthifolius* followed by dark-capped bulbuls, speckled mousebirds and Cape white-eyes. This indicated that although all avian species had similar germination success, Cape white-eyes would most likely promote the least seed germination and dispersal (at least on an individual basis) as their fruit consumption is limited by their bill and body size. Dark-capped bulbuls and speckled mousebirds most likely affect germination success and dispersal in more or less the same manner. Red-winged starlings are most likely to have the greatest effect on germination success and dispersal. The germination potential of each avian species in this study was only considered on the basis of that of individual birds. It would be interesting to see how effective the respective avian species are as seed dispersers of *S. terebinthifolius* in the wild given their respective abundances and distributions.

5. Conclusion

Our study showed that the native avian frugivorous species play a role in the dispersal and germination of the invasive plant *S. terebinthifolius* by not only decreasing germination time, but also increasing germination success through pulp removal. It is also clear that, although all the avian species used in this study had more or less the same effect on germination time and percentage, their variances in body and bill size could potentially mean that larger birds (such as red-winged starlings, dark-capped bulbuls and speckled mousebirds) play a greater role in seed dispersal as they ingest a greater number of seeds. Further studies on the invasive biology of *L. glutinosa* need to be conducted in order to determine the mechanisms by which this invasive plant establishes populations as this study was unable to make conclusions about the role that native avian frugivores may play. In Thailand the seeds were dispersed mainly by birds (Ratree, 2006). It may also be interesting to see if rodents do indeed feed on *L. glutinosa* seeds as speculated. The important role that avian frugivores play in the seed dispersal and germination success of the invasive plant *S. terebinthifolius* is evident, especially in the absence of native fruiting plants. The results from this study could be useful in future management efforts to minimize the impact of invasive plant species, perhaps by removing and replacing them with native fruiting plants.

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