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# Knysna Turacos (*Tauraco corythaix*) do not improve seed germination of ingested fruit of some indigenous South African tree species

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## Abstract

Seed dispersal plays an important role in the persistence, regeneration and maintenance of plant communities. It is therefore not surprising that much attention has been paid to the germination potential of seeds ingested by frugivorous animals. Consequently the aim of this study was to determine what effect ingestion of seeds by Knysna Turacos (*Tauraco corythaix*) has on the germination rate and germination percentage of indigenous South African tree species. Fruits from twelve tree species were fed to the Turacos in separate trials and seed retention times were determined as it has been suggested that a longer seed retention time may increase germination rates. At the end of each trial, seeds were extracted from excreta of individual birds and planted in trays containing potting soil. Germination was recorded daily until 14 days of no germination. Knysna Turacos seed retention times were in the range of those obtained by other studies, with *Ficus sur* seeds having the fastest retention times ( $12.4 \pm 0.8$  min) and *Celtis africana* the slowest ( $34.6 \pm 5.6$  min). Seed ingestion by Knysna Turacos did not influence the rate at which seeds germinated in 83% of the tree species, but ingested *Ficus lutea* and *Ficus natalensis* seeds germinated significantly sooner than whole fruit seeds. Future studies relating the composition of indigenous forest fruits to food preferences of Knysna Turacos may give insight into their role as potential seed dispersers of indigenous fruiting tree species.

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**Keywords:** Germination percentage; Germination rate; Indigenous trees; Knysna Turacos; Seed retention

## 1. Introduction

Seed dispersal plays a vital role in the persistence, regeneration and maintenance of plant communities (Bascombe and Jordano, 2007; Chave et al., 2002; Herrera, 2003; Nathan and Muller-Landau, 2000). Up to 90% of tropical and between 30 and 50% of temperate tree species rely on frugivorous animals to disperse their seeds (Aizen et al., 2002; Herrera, 2003). It is therefore not surprising that much attention has been paid to the germination potential of seeds ingested by frugivorous animals (reviewed in Traveset, 1998). According to Ridley (1930), ornithochory is a process of seed dispersal by avian frugivores where fruit pulp is consumed and viable seeds are regurgitated or defecated. The ingestion of seeds by frugivores is assumed to enhance and

increase germination success and rate (defined as the speed at which seeds germinate; Traveset et al., 2001) respectively (Krefting and Roe, 1949; Traveset and Verdú, 2002; Turcek, 1963).

Many studies have found that seeds ingested by frugivores experience higher germination success compared with that of non-ingested seeds (Barnea et al., 1990, 1991; Clergeau, 1992; Ellison et al., 1993; Izhaki and Safriel, 1990; Murray et al., 1994). The removal of the pulp has been suggested to enhance germination as germination inhibitors may be present in the pulp (Cipollini and Levey, 1997). Seeds from which the pulp has been removed may also have reduced risks of predation and/or microbial attacks (Barnea et al., 1991; Herrera, 1984; Izhaki and Safriel, 1990; Witmer and Cheke, 1991). Modification of the seed coat structure (either chemically or mechanically) due to ingestion has also been suggested to enhance germination (Barnea et al., 1990; Izhaki and Safriel, 1990; Yagihashi et al., 1998).

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Seed ingestion by frugivores has also been shown to decrease (Crossland and Vander Kloet, 1996; Nogales et al., 1995; Smith, 1975; Valido and Nogales, 1994) or have no significant effect on germination success (Barnea et al., 1992; Clout and Tilley, 1992; Howe and Vande Kerckhove, 1981; Stocker and Irvin, 1983).

Studies have shown that ingestion of seeds can increase (Noble, 1975; Swank, 1944) or decrease (Ellison et al., 1993; Nogales et al., 1995) the rate of germination and can cause a total loss of seed viability (Hudler et al., 1979). Some plant species, however, are completely reliant on ingestion by frugivorous animals for germination (Noble, 1975).

The effect of ingestion on germination success differs between both plant and animal species and may be as a result of factors such as differing gut retention times and the resulting level of scarification of the endocarp; and the composition of the seed coat (Barnea et al., 1990, 1991; Izhaki and Safriel, 1990; Krefting and Roe, 1949; Traveset 1998; Traveset et al., 2001; Yagihashi et al., 1998).

Seed retention time (SRT) can be defined as the time spent passing through the bird's digestive system i.e. the time from when the bird ingests a fruit to the time when the seed is defecated or regurgitated (Fukui, 2003). It has been suggested that a longer SRT is more beneficial in that the level of scarification of the seed coat is increased and subsequently germination rates are enhanced (Barnea et al., 1991; Fukui, 2003). This however, may be an oversimplification of this relationship. Different seed sizes have different retention times with small seeds tending to have longer SRTs (Fukui, 2003; Traveset and Verdú, 2002). Ingested small seeds are therefore more likely to have an increased germination success (Traveset and Verdú, 2002).

Knysna Turacos (*Tauraco corythaix*) (Musophagiformes: Musophagidae) are relatively large (c. 310 g) fairly common forest frugivores (Oatley, 1997) that are endemic to South Africa (Du Plessis and Dean, 2005; Rowan, 1983). They may track fruit locally in response to availability (Rowan, 1983).

The aim of this study was to determine what effect ingestion of seeds by Knysna Turacos has on the percentage germination and rate of germination of indigenous South African tree species. It was predicted that percent germination and rate of germination of ingested seeds would be greater for most of the indigenous species than for pulp removed and whole fruit seeds. Seed retention time was also measured in order to determine the potential effect on germination success.

## 2. Materials and methods

### 2.1. Bird capture and maintenance

Six captive-bred Knysna Turacos were sourced from Mr. M. C. Weber under permit from Ezemvelo KZN Wildlife (permit number: 1781/2008). Before experiments were conducted the birds were housed in pairs in outside aviaries (1 × 2.12 × 2.66 m).

Birds were fed a maintenance diet (a choice of mealworms (*Tenebrio molitor* larvae), carrots, apples, papayas, pears, bananas, oranges and/or grapes) daily. Skin was removed

from papayas, oranges and bananas and the fruit was then cut into c. 1 × 1 × 1 cm cubes. The other fruits were grated. A mixture of Aviplus Softbill/Mynah crumble and pellets (Avi-products, Durban, South Africa) was added to the maintenance diets daily. Water was provided ad libitum.

### 2.2. Plant species

Fruits from a range of indigenous tree species (n=12) (Table 1) were used. Trees were sourced from the KwaZulu-Natal coastal and afro-montane indigenous forests and fruits were used within 48 h of collection. The availability of fruit limited the choice of tree species used in this study.

### 2.3. Experiments

Birds were moved indoors for 2 days before any trials were conducted. Here they were housed in individual cages (42.7 × 43 × 59.3 cm) in a constant environment room with a 12L:12D photoperiod at 25 ± 1 °C. To ensure a post-absorptive state at the beginning of each experiment, any uneaten food was removed at 1800 h and no food was available overnight. Clean plastic trays, the same size as the cage's base, were placed under each cage prior to 0600 h. Water was provided ad libitum.

### 2.4. Seed retention time

Indigenous fruit for each specific trial was added to the birds' maintenance diet 1 day prior to each experimental day. On the experimental days, birds were provided with whole fruits of a particular tree species. The length of the trials for each particular fruit species varied from 6 to 12 h depending on fruit availability and the amount eaten. The time that the birds first ingested the fruit including the seed and the first appearance of seeds in their excreta was recorded to determine SRTs. Excreta were collected from the plastic trays at the end of each trial.

### 2.5. Germination success

Seeds were extracted from the respective individual birds' excreta from each fruit treatment and planted in separate trays (265 × 180 × 75 mm) containing potting soil within 24 h after the feeding trial experiment (Table 2). The seeds were not washed prior to planting. Regurgitated seeds were easily identifiable as they were of a different colour from the defecated seeds or, in some cases, had little bits of pulp still attached. Seeds were covered with a potting soil layer c. 0.5 cm deep. Trays were housed in a shade house and watered daily. Germination was considered as when the seedlings first emerged through the soil surface and were visible. Germination was recorded daily for 90 days. If 100% germination had not occurred by day 90, trials were continued for a further 14 days. If germination was still taking place after day 104, trials were continued until 14 days of no germination occurred. Counted seedlings were removed. Controls of whole fruits and manually pulp removed seeds were planted concurrently and in the same manner. These controls were used in order to determine what effects the removal of pulp

Table 1  
Fruit characteristics of indigenous South African tree species used in the study.

Tree species	Family*	Fruiting period*	Colour when ripe*	Fruit size* ( <sup>a</sup> =mm; <sup>b</sup> =mm diameter)	Fruit size rank <sup>#</sup>	Seed size* (mm)	Seed size rank <sup>^</sup>	Mean±SE number of seeds
<i>Bridelia micrantha</i>	Euphorbiaceae	Nov–April	Black	10×7 <sup>a</sup>	3	5×3	4	1.0±0.0 (5)
<i>Celtis africana</i>	Celtidaceae	Oct–April	Brownish-yellow	8 <sup>b</sup>	2	7×5	6	1.0±0.0 (5)
<i>Clerodendrum glabrum</i>	Verbenaceae	Feb–July	Yellowish white	10 <sup>b</sup>	4	8×2	7	1.0±0.0 (5)
<i>Ficus lutea</i>	Moraceae	June–Oct	Yellowish brown	15–30 <sup>b</sup>	9	1.5×1	1	124.0±17.3 (5)
<i>Ficus natalensis</i>	Moraceae	All year	Red-brown	10–20 <sup>b</sup>	7	1.5×1	1	168.8±35.7 (5)
<i>Ficus petersii</i>	Moraceae	Aug–Dec	Red	10 <sup>b</sup>	4	1.5×1	1	94.6±9.0 (5)
<i>Ficus sur</i>	Moraceae	All year	Orange-red	20–40 <sup>b</sup>	10	1.5×1	1	828.0±50.6 (5)
<i>Grewia occidentalis</i>	Tiliaceae	Jan–July	Reddish purple	25 <sup>b</sup>	8	7×5	6	2.3±1.7 (5)
<i>Mimusops caffra</i>	Sapotaceae	All year	Red	20×15 <sup>a</sup>	6	15×10	8	1.0±0.0 (5)
<i>Rhamnus prinoides</i>	Rhamnaceae	Jan–Aug	Purplish black	6 <sup>b</sup>	1	4×4	1	3.0±0.0 (5)
<i>Solanum giganteum</i>	Solanaceae	Feb–July	Shiny red	10 <sup>b</sup>	4	4×3	2	12.2±1.5 (5)
<i>Syzygium cordatum</i>	Myrtaceae	Oct–June	Deep purple	20×10 <sup>a</sup>	5	7×4	5	1.0±0.0 (5)

Note: numbers in parentheses are sample sizes.

<sup>#</sup>1 = smallest, 10 = largest; <sup>^</sup>1 = smallest, 8 = largest.

\*Griffiths and Lawes (2006), Boon (2010).

and/or the scarification of the seeds have on germination success. Five fresh fruits of each species were dissected to determine the mean number of seeds in the whole fruits in order to determine germination percentages.

## 2.6. Analyses

The cumulative percentage germination was determined for each tree species. Average number of seeds per whole fruit for each tree species was used to calculate germination percentage (Table 1). Seed retention and the time taken from the time of sowing until first seedling emergence for each plant species were analysed using Kruskal–Wallis ANOVA tests. Kruskal–Wallis ANOVA tests were also used to determine if there were significant differences between ingested, regurgitated (where applicable), pulp removed and seeds in whole fruits. The relationship between seed size and retention time was analysed using a simple linear regression. All analyses were conducted using STATISTICA (Statsoft, Tulsa, version 7, USA). Mean±SE

was reported for all values and Bonferroni adjustments were made.

## 3. Results

### 3.1. Fruit traits

Fruits used in this study varied in a number of features such as colour when ripe, fruit size, seed size, and mean number of seeds per fruit (Table 1).

### 3.2. Seed retention time

The SRTs varied significantly between the different tree species (Kruskal–Wallis ANOVA  $H_{11}=24.862$ ,  $n=72$ ,  $p<0.01$ ) (Fig. 1). *Ficus sur* seeds had the fastest retention times ( $12.4±0.8$  min) whilst *Celtis africana* had the slowest ( $34.6±5.6$  min). The relationship between seed size and retention time was not significant ( $r^2=0.167$ ,  $F=3.21$ ,  $p=0.104$ ,  $df=10$ ).

Table 2  
Number of seeds planted in soil trays for each indigenous South African tree species fed to Knysna Turacos.

Tree species	Ingested/ regurgitated	Number of seeds per tray	Number of trays	Number of pulp removed seeds in control	Number of whole fruits in control
<i>Bridelia micrantha</i>	Ingested	167	6	410	410 (1.0±0.0)
	Regurgitated	20			
<i>Celtis africana</i>	Ingested	100	6	360	360 (1.0±0.0)
<i>Clerodendrum glabrum</i>	Ingested	40	6	40	40 (1.0±0.0)
<i>Ficus lutea</i>	Ingested	50	6	50	1 (124.0±17.3)
<i>Ficus natalensis</i>	Ingested	30	6	30	1 (168.8±35.7)
<i>Ficus petersii</i>	Ingested	50	6	50	1 (94.6±9.0)
<i>Ficus sur</i>	Ingested	50	6	50	1 (828.0±50.6)
<i>Grewia occidentalis</i>	Ingested	24	6	24	11 (2.3±1.7)
<i>Rhamnus prinoides</i>	Ingested	50	6	140	47 (3.0±0.0)
	Regurgitated	36	3 <sup>a</sup>		
<i>Solanum giganteum</i>	Ingested	30	6	30	3 (12.2±1.5)
<i>Syzygium cordatum</i>	Ingested	30	6	170	170 (1.0±0.0)
	Regurgitated	20			

Note: numbers in parentheses are mean±SE number of seeds per fruit ( $n=5$ ).

<sup>a</sup> Only 3 Knysna Turacos regurgitated *R. prinoides* seeds.

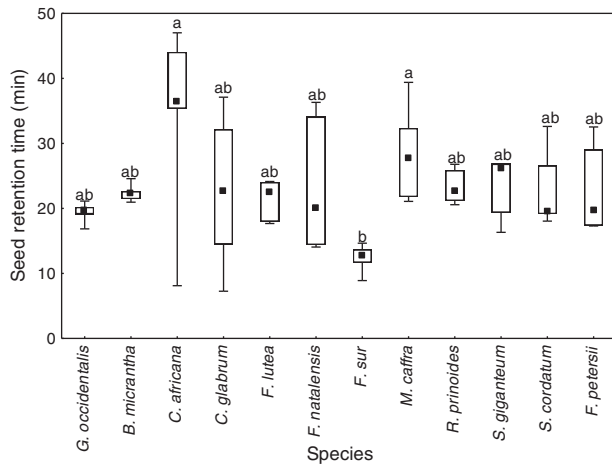


Fig. 1. Seed retention time for fruit of indigenous tree species eaten by Knysna Turacos ( $n=6$ ). (Boxes indicate the 25 and 75% quartiles; solid black squares the medians; and bars the 10 and 90% values. Treatments with letters in common were not significantly different at the 5% level. See Table 1 for tree species details.)

### 3.3. Germination percentage

Ingested seed percentage germination varied significantly between the tree species (Kruskal–Wallis ANOVA  $H_{11}=53.934$ ,  $n=72$ ,  $p<0.01$ ) (Fig. 2). Mean percentage germination of ingested seeds ranged from  $12.0\pm 3.6$  (*Rhamnus prinoides*) to  $94.5\pm 4.6\%$  (*Bridelia micrantha*), which was not significantly different to pulp removed and whole fruit seeds (Figs. 3 and 4).

Regurgitated seed percentage germination varied significantly between the tree species (Kruskal–Wallis ANOVA  $H_2=8.424$ ,  $n=15$ ,  $p=0.015$ ) (Fig. 5). Mean regurgitated seed percentage germination ranged from  $4.6\pm 2.5$  (*R. prinoides*) to  $94.2\pm 5.8\%$  (*Syzygium cordatum*), which was not significantly different to ingested, pulp removed and whole fruit seeds (Figs. 3 and 4).

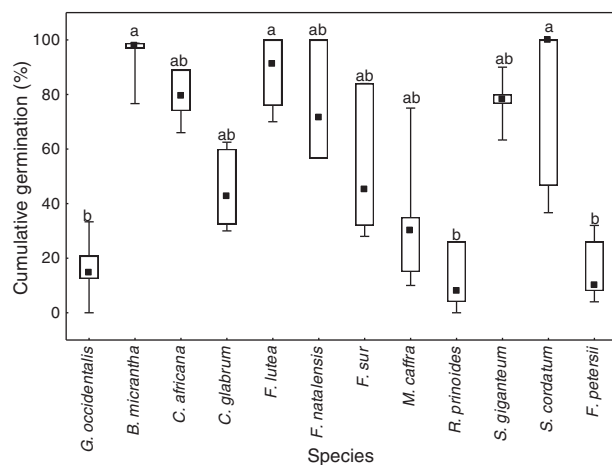


Fig. 2. Cumulative germination percentage for indigenous seeds ingested by Knysna Turacos. (Boxes indicate the 25 and 75% quartiles; solid black squares the medians; and bars the 10 and 90% values. Treatments with letters in common were not significantly different at the 5% level.)

### 3.4. Mean time to seedling emergence

Seedling emergence from ingested seeds varied significantly among the tree species (Kruskal–Wallis ANOVA  $H_{11}=58.871$ ,  $n=72$ ,  $p<0.01$ ) (Fig. 6a). The mean time for emergence of seedlings from ingested seeds ranged from  $12.3\pm 0.7$  (*B. micrantha*) to  $57.7\pm 7.1$  days (*C. africana*), which was not significantly different to seedling emergence from pulp removed seeds for all the tree species (Figs. 3 and 4). However, in the case of *F. lutea* and *F. natalensis*, it was significantly higher than mean seedling emergence from whole fruit seeds (Figs. 3 and 6a).

Seedling emergence from regurgitated seeds did not vary significantly between the tree species (Kruskal–Wallis ANOVA  $H_2=3.425$ ,  $n=15$ ,  $p=0.180$ ) (Fig. 6b). The mean time for emergence of seedlings from regurgitated seed ranged from  $12.0\pm 0.0$  (*B. micrantha*) to  $22.0\pm 11.4$  days (*R. prinoides*), which was not significantly different to seedling emergence from ingested and pulp removed seeds (Figs. 3 and 4). However, in the case of *B. micrantha*, it was significantly higher than mean seedling emergence from whole fruit seeds (Figs. 3 and 6b).

## 4. Discussion

Different sized seeds are expected to have different retention times in a birds' gut (Fukui, 2003), with small and light seeds generally retained longer than large and heavy seeds (Garber, 1986; Gardener et al., 1993; Levey and Grajal, 1991). This was contrary to the current study where small *F. sur* seeds had the fastest ( $12.36\pm 0.84$  min) and the larger *Celtis africana* seeds the slowest ( $34.55\pm 5.63$  min) retention times although this relationship was not found to be significant. Retention times have been suggested to decrease as the number of fruit eaten increases (Murphy et al., 1993). This could explain the inconsistent results obtained in this study, as it was observed that *C. africana* fruits were smaller and contained less pulp than *F. sur* fruits (pers. ob.). Seed retention times in the current study were similar to those obtained by Barnea et al. (1991) for blackbirds, *Turdus merula* (15–74 min) and bulbuls, *Pycnonotus xanthopygos* (12–27 min); Linnebjerg et al. (2009) for red-whiskered bulbuls, *Pycnonotus jocosus* (13–68 min); and by Fukui (2003) for brown-eared bulbuls, *Hypsipetes amaurotis* (2–123 min).

In order to increase their ingestion rates, frugivorous birds tend to have short gut passage times (Levey, 1991), but these may vary for various reasons. However, a longer SRT may be more beneficial to plant fitness in terms of increased germination and longer dispersal distances (Barnea et al., 1991; Fukui, 2003). This suggests that, in this study, *C. africana* seeds would have the highest germination percentage and potential dispersal and *F. sur* seeds the lowest. This, however, was not found as *B. micrantha* seeds had the highest and *R. prinoides* the lowest germination percentage with *C. africana* and *F. sur* experiencing germination percentages between this, i.e. *B. micrantha* and *R. prinoides* had similar retention times.

Ingestion by birds has been suggested to enhance seed germination by either depulping the seeds (Robertson et al., 2006) or by seed coat abrasion (Agami and Waisel, 1986;

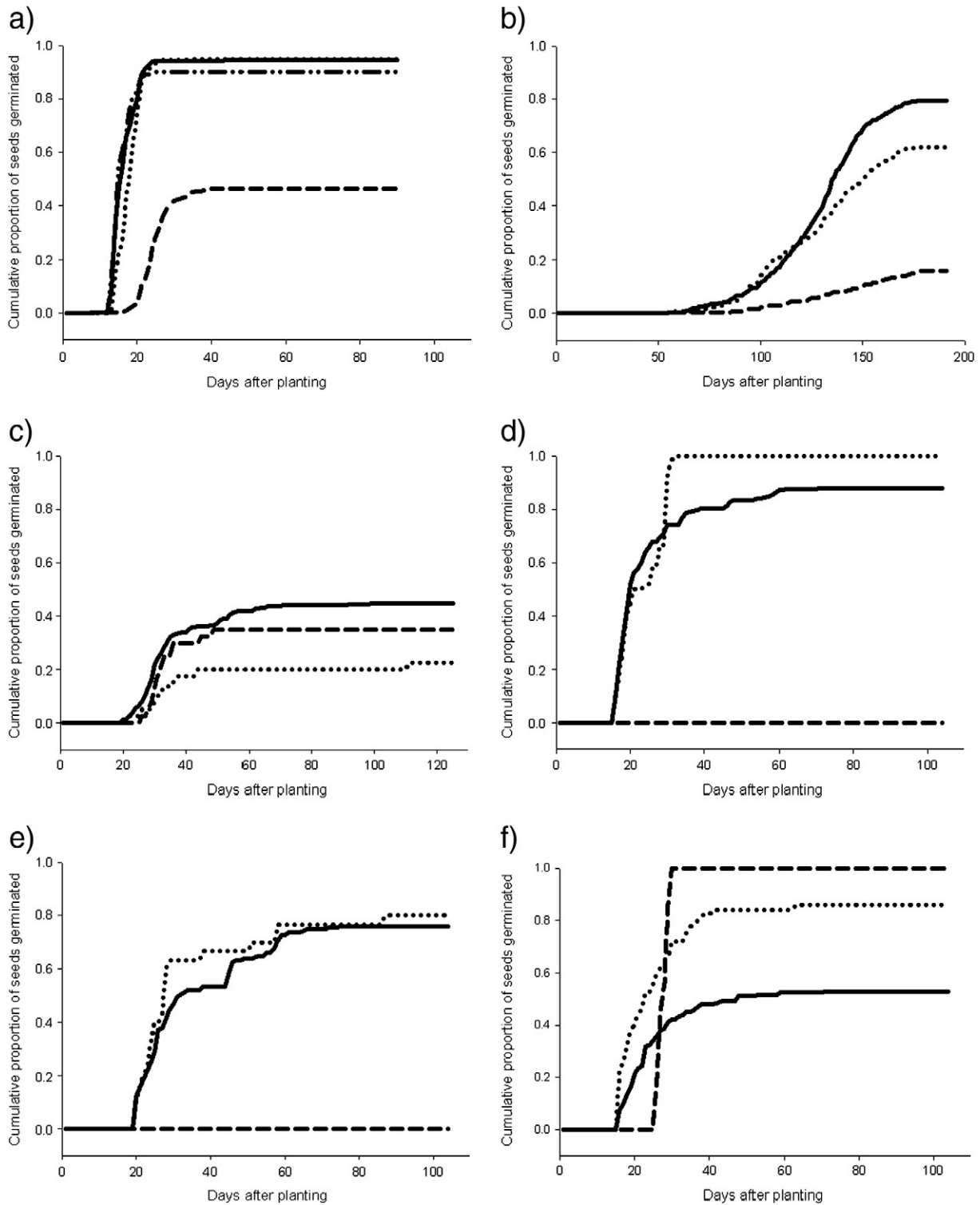


Fig. 3. Mean cumulative percentage germination for ingested (—), regurgitated (····), pulp removed (---) and whole fruit (-·-·) seeds from a) *B. micrantha* after 90 days; b) *C. africana* after 191 days; c) *C. glabrum* after 125 days; d) *F. lutea* after 104 days; e) *F. natalensis* after 104 days; and f) *F. sur* after 104 days.

Traveset, 1998). Interestingly, ingestion by Knysna Turacos did not have any significant effect on seed germination percentage. Percentage germination of ingested seeds was not significantly different to that of pulp removed seeds. As seed coat abrasion was not assessed in this study we therefore tentatively suggest that, in this study, seed coat abrasion does not influence

germination. This may be due to the species of seeds used as certain seeds possess coat imposed or mechanical dormancy whilst others possess physiological dormancy and still others have no dormancy mechanisms (Kelly et al., 1992). The ability of ingestion to influence germination therefore depends on the kind of dormancy a seed has, if any (Kelly et al., 1992).

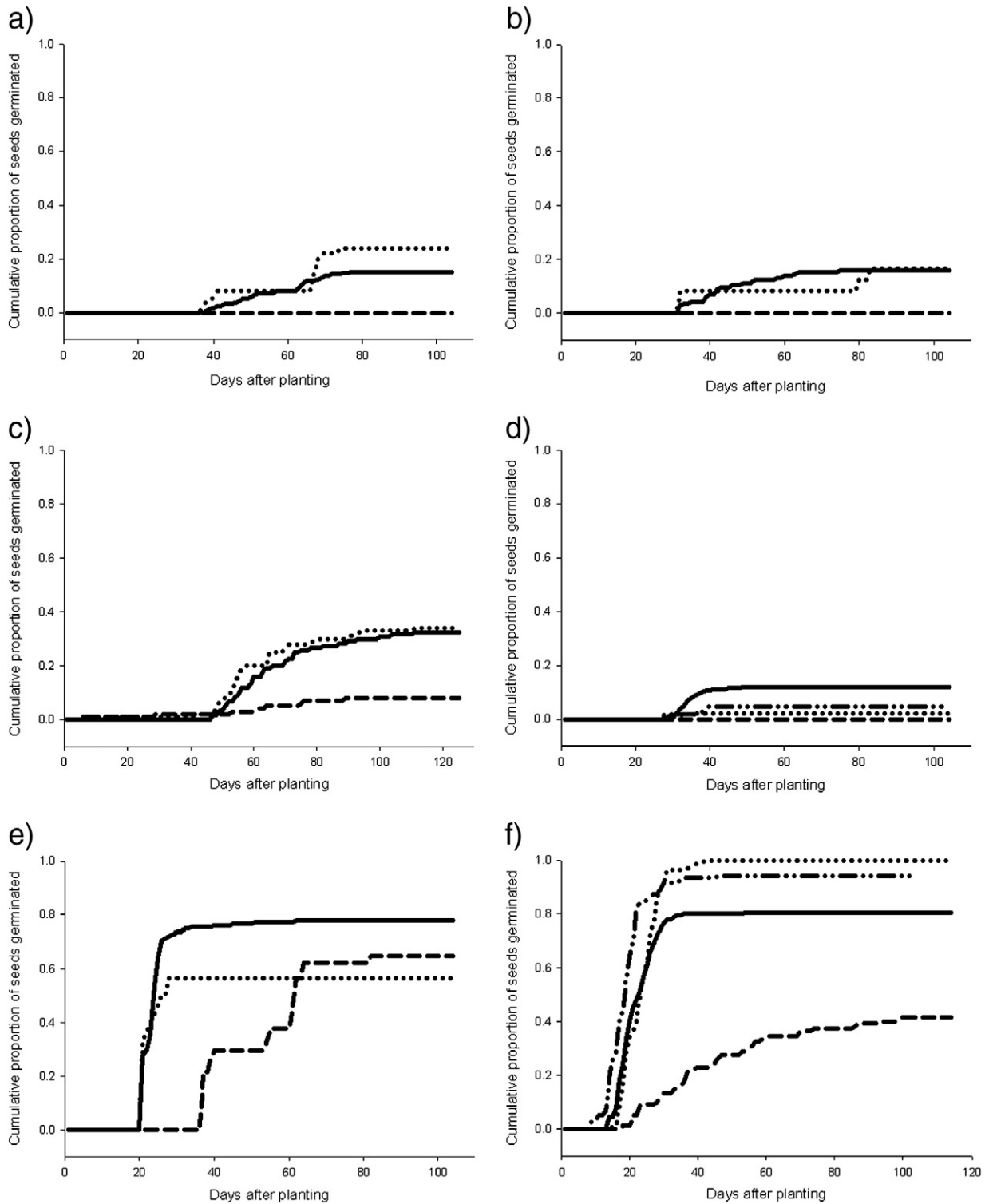


Fig. 4. Mean cumulative percentage germination for ingested (—), regurgitated (···), pulp removed (---) and whole fruit (-·-·) seeds from a) *F. petersii* after 104 days; b) *G. occidentalis* after 104 days; c) *M. caffra* after 125 days; d) *R. prinoides* after 104 days; e) *S. giganteum* after 104 days; and f) *S. cordatum* after 114 (ingested, pulp removed and whole fruit) and 104 (regurgitated) days.

Percentage germination of ingested seeds was also not significantly different to that of whole fruit seeds, suggesting that pulp removal did not enhance percentage germination. Interestingly, many more whole fruit seeds from *F. sur* germinated than ingested seeds.

Seed ingestion by Knysna Turacos did not influence the rate at which seeds germinated in all tree species except ingested *F. lutea*, and *F. natalensis* seeds which germinated significantly sooner than whole fruit seeds. Interestingly, whole fruit seeds from *F. sur* germinated faster than ingested seeds. Regurgitation

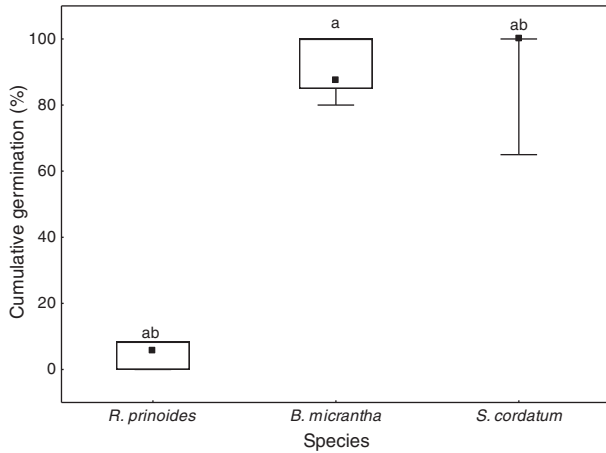


Fig. 5. Cumulative percentage germination for indigenous seeds regurgitated by Knysna Turacos. (Boxes indicate the 25 and 75% quartiles; solid black squares the medians; and bars the 10 and 90% values. Treatments with letters in common were not significantly different at the 5% level.)

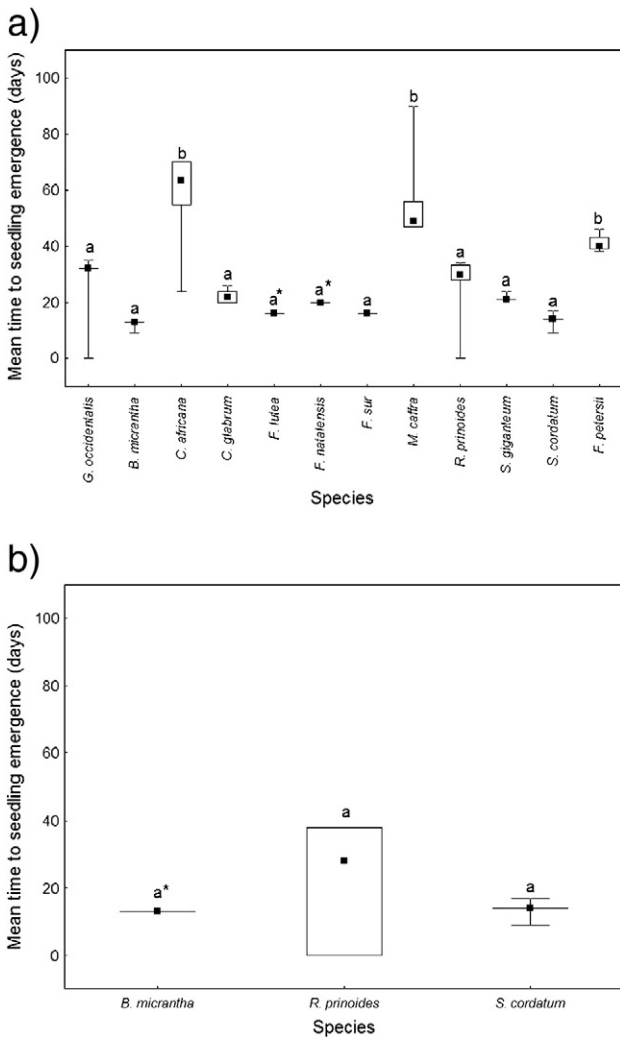


Fig. 6. Day of first seedling emergence for indigenous seeds a) ingested and b) regurgitated by Knysna Turacos. (Boxes indicate the 25 and 75% quartiles; solid black squares the medians; and bars the 10 and 90% values. Treatments with letters in common were not significantly different at the 5% level. Note: \* indicates a significant difference when compared with whole fruit seeds.)

of seeds by Knysna Turacos did not influence the rate at which seeds germinated in all relevant tree species except regurgitated *B. micrantha* seeds which germinated significantly sooner than whole fruit seeds. The species of seed, its requirements for germination and whether the seed is damaged during the ingestion process will all influence the impact of ingestion on seed germination. A faster germination rate may be beneficial in terms of an advantage in seedling size and therefore a greater chance of survival and also in terms of reducing the risk of the seeds being predated (Traveset et al., 2001). These results are similar to those obtained by Barnea et al. (1991), Izhaki and Safriel (1990), and Traveset and Willson (1997) who found no significant effect on rate of germination of seeds ingested by various avian frugivores.

In conclusion, Knysna Turacos had seed retention rates that were in the range of those obtained by other studies for other frugivores and plant species. Furthermore their ingestion of seeds generally did not enhance percentage germination, however, as ingestion did not reduce germination it could still be considered an important dispersal mechanism. The ingestion of seeds also did not generally enhance rate of germination except for ingested *F. lutea* and *F. natalensis* seeds which germinated significantly sooner than whole fruit seeds. Interestingly, only whole fruit seeds from *F. sur* germinated faster and had many more germinated than ingested seeds. Consequently we reject our predictions for all tree species except for *F. lutea* and *F. natalensis*. Future studies relating the composition of indigenous forest fruits to food preferences of Knysna Turacos may give insight into their role as potential seed dispersers of indigenous fruiting tree species.

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