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An appraisal of seed enumeration and videographic techniques for determining seed removal rates by birds

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Abstract

We examined the efficacy of seed enumeration and videographic techniques for determining seed removal by birds from indigenous (*Chrysanthemoides monilifera* and *Olea europaea* subsp *africana)* and alien (*Lantana camara* and *Solanum mauritianum)* shrubs at different study sites in the Cape Floristic Region. The seed enumeration technique involved counting the numbers of fruits and associated seeds removed monthly by birds, excluding those naturally abscised, from the shrub canopy. The videographic technique involved visual counts from images of the numbers of fruits and associated seeds consumed by birds over specific time intervals captured by a digital camcorder. Daily seed removal rates by all birds, irrespective of species, measured by both techniques were similar with no significant interactions evident between measuring techniques, site and shrub species. Both techniques displayed higher seed removal from tiny-seeded *S. mauritianum* than other shrub species; this was also evident among individual bird species. However, the seed enumeration technique was unable to discriminate between foraging organisms, contamination of traps by wind-blown fruits abscised from neighbouring branches and fruit theft from the canopy and the traps. In contrast, the videographic technique provided permanent visual and time-lapse records for individual foraging bird species allowing greater measurement precision and interpretation of fruit removal behaviour by birds. We recommend use of the videographic technique over the seed enumeration technique for studying vertebrates' seed removal in a detailed manner.

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Résumé

Nous avons examiné l'efficacité de la technique de dénombrement des semences et de la technique vidéographique pour déterminer le prélèvement, par les oiseaux, de semences provenant de buissons indigènes (*Chrysanthemoides monilifera* et *Olea europaea subsp africana*) et exotiques (*Lantana camara* et *Solanum mauritianum*) sur différents sites d'études de la Région floristique du Cap. La technique de dénombrement des semences impliquait de compter le nombre de fruits, et des semences associées, prélevés chaque mois par les oiseaux à la canopée des buissons, à l'exclusion de ceux qui sont tombés naturellement. La technique vidéographique impliquait des comptages visuels, à partir d'images captées par un caméscope digital, du nombre de fruits et des semences associées consommés par les oiseaux à intervalles déterminés. Les taux journaliers de prélèvement des semences par tous les oiseaux, quelle que soit leur espèce, mesurés selon les deux techniques, étaient semblables, sans interactions significatives visibles entre les techniques de mesure, les sites et les espèces de buissons. Les deux techniques révélaient un prélèvement plus important de *S. mauritanium*, aux graines minuscules, que d'autres espèces d'arbustes. Ceci était aussi très clair entre chaque espèce d'oiseaux. Cependant, la technique de dénombrement des semences ne permettait pas de faire la distinction entre les organismes consommateurs, la contamination des pièges par des fruits détachés de branches voisines par le vent, le vol des

fruits dans la canopée et les pièges. Par contre, la technique vidéographique fournissait un compte-rendu visuel régulier et permanent pour chaque espèce d'oiseau consommateur, ce qui permet une plus grande précision et une meilleure interprétation du comportement des oiseaux qui se nourrissent des fruits. Nous recommandons d'utiliser la technique vidéographique plutôt que le dénombrement des semences pour étudier de façon détaillée le prélèvement des semences par des vertébrés.

Introduction

A better understanding of the effectiveness of bird-mediated seed dispersal of fleshy-fruited plants could elucidate population dynamics of natural plant communities invaded by alien shrubs and trees, such as those in the South African Cape Floristic Region (Mokotjomela, Musil & Esler, 2013a). It has been suggested that high preference by frugivorous birds for fleshy fruits of alien shrubs species because of high sugar content might limit seed dispersal services for native shrub species (Gosper, Stansbury & Vivian-Smith, 2005; Mokotjomela, Musil & Esler, 2013a), and thus increase their vulnerability to extinction (Trakhtenbrot *et al.*, 2005; Schurr *et al.*, 2007). Important local avian seed dispersers exhibit higher foraging visitation frequency indices on fruits of emerging alien shrub species than those of established alien and the native shrub species (Mokotjomela, Musil & Esler, 2013b). Indeed, studies have shown that most invasive alien shrub species are dispersed by birds (Knight, 1988; Gosper, Stansbury & Vivian-Smith, 2005; Vittoz & Engler, 2007; Mokotjomela *et al.*, 2013c).

Studies have used different empirical techniques for collecting data on seed removal by birds (Sallabanks, 1993; Nathan, 2001; Bullock, Shea & Skarpaas, 2006). For instance, Knight (1988) marked fleshy fruits of alien and native shrub species and monitored their rates of removal by birds through counting remaining fruits every day and on a weekly basis. Sallabanks (1993) estimated the numbers of seeds removed by birds as the difference between the seeds initially counted in a portion of tree canopy and those collected in the seed traps placed beneath the tree canopy plus those still left in the tree. Jordano & Schupp (2000) recorded the numbers of birds species foraging on fruits and counted the numbers of seeds removed as well as the number of exit flights from the focal trees so that the rate of seed removal and dispersal per visit could be calculated. More recently with the development of digital camcorders, videographic techniques have been applied to measure fruit and seed consumption by vertebrates including birds (Spiegel & Nathan, 2007; Kays *et al.*, 2011; Mokotjomela & Hoffmann, 2013). However, some plants have dispersal vectors other than birds (e.g. mammals, Higgins, Nathan & Cain, 2003; Dennis & Westcott, 2006), which suggests that observational quantitative measurements of seed removal by birds might be underestimates of total dispersal, while seed enumeration may provide a more accurate measure of nonspecies-specific dispersal rates (Bullock, Shea & Skarpaas, 2006; Schurr *et al.*, 2009). For example, fleshy fruits of common hawthorn (*Crataegus monogyna*) display adaptation to dispersal by birds, but they are often dispersed by nonstandard vectors such as rivers and harvesting by human beings (Ridley, 1930; Higgins, Nathan & Cain, 2003). The effectiveness of different techniques for measuring seed removal might also be influenced by spatial scale, fruiting patterns, bird foraging strategies and erratic behaviour of birds in different vegetation types (Snow, 1981; Bullock, Shea & Skarpaas, 2006; Carlo, Aukema & Morales, 2007). In fact, similar techniques have yielded different results for comparable environmental conditions, plant and bird species (Nathan, 2001; Bullock *et al.*, 2003; Bullock, Shea & Skarpaas, 2006). While there may be a real difference in foraging rates, there is potential for the reliability of the exact methods used in each study to have affected the results, which also provide knowledge gap for our study. Other studies have attributed such differences partly to multiple interactions between frugivorous bird species with different fruit processing techniques and body sizes which influence numbers of fruits ingested (Jordano, 2000), and the characteristics of the fruiting plant species as well as their location (Dennis & Westcott, 2006; Carlo, Aukema & Morales, 2007). The lack of consistency among different techniques used to measure the quantities of seeds removed by birds and their potential dispersal distances preclude generalizations. However, direct observations in measuring seed dispersal by birds (Jordano & Schupp, 2000) coupled with other methods can be useful in establishing the reliability of different techniques (Bullock, Shea & Skarpaas, 2006).

We compared the effectiveness of direct seed enumerations, including the use of fruit traps and videographic behavioural observation techniques in quantifying seed removal by frugivorous bird species from coexisting fleshy-fruited native and alien shrub species in the South African Mediterranean climate region (Mokotjomela, Musil & Esler, 2013a). Seed enumeration techniques have entailed direct counts of the numbers of fruits consumed by birds over specific time intervals coupled with placement of fruit traps underneath the plant canopies to measure fruit loss by abscission (Sallabanks, 1993; Korine, Kalko & Herre, 2000; Bache & Kelly, 2004), while videographic technique entailing use of digital camcorder was applied to measure fruit and seed consumption by birds (Spiegel & Nathan, 2007; Kays *et al.*, 2011; Mokotjomela & Hoffmann, 2013). Indeed, surveillance digital camera traps are currently recommended for studying wildlife in a detailed and nonintrusive manner (Kays *et al.*, 2011). The efficacy and practicality of the seed enumeration and videographic techniques in elucidating seed removal by birds have not been compared, and this knowledge gap formed another basis of this study. We tested a hypothesis that birds are the primary vector of seed dispersal of especially alien fleshy-fruited shrub species in the Cape Floristic Region and that other vectors contribute negligibly to seed removal rate. We predicted that videographic (species-specific) and seed enumeration (nonvector-specific) data should not give significantly different seed removal rate results.

Methods and materials

Study sites, shrub and bird species

Seed removal by frugivorous bird species that visited and ingested seeds of focal plants were examined at four study sites, each site comprising mixed populations of alien and indigenous shrubs, located on different vegetation units described in Mucina & Rutherford (2006). The sites were Hout Bay located in Peninsula Granite Fynbos, Paarl located in Swartland Shale Renosterveld, Hermanus located in Overberg Sandstone Fynbos and Swellendam located in Breede Shale Renosterveld (Swellendam). Each site contained populations of two indigenous shrubs, bietou (*Chrysanthemoides monilifera*) and African olive (*Olea europaea africana*), intermixed with two alien shrubs, Lantana (*Lantana camara*) and Bugweed (*Solanum mauritianum*). Each of these species produces fleshy fruits. As vegetation composition strongly influences fruit and seed removal rates by birds (Carlo, Aukema & Morales, 2007), all shrub species were selected based on their co-occurrence over a wide range of natural vegetation types, their overlapping fruiting times (Van Wyk & van Wyk, 1997) and consumption of their fruit by local frugivorous birds (Richardson & Fraser, 1995).

Seed enumeration technique

Measurements were conducted in autumn of 2009 and in autumn of 2010 when all shrub species were fruiting. The bird species that foraged on the selected shrubs included the tiny (<30 g) Cape white-eye (*Zosterops pallidus*), the small (30–50 g) Cape bulbul (*Pycnonotus capensis*), the medium (50–150 g) size olive thrush (*Turdus olivaceus*) and speckled mousebird (*Colius striatus*), and the large (>150 g) African olive-pigeon (*Columba arquatrix*). Labelled tags were affixed to four fruiting branches on 15 individuals of each shrub species at each site. Horizontal and vertical canopy dimensions of the shrubs to which the labelled tags were affixed were measured and their fruiting canopy areas calculated as a fraction of the total area of the tree containing fruits. The entire canopies of *C. monilifera, L. camara* and *O. africana* were occupied in fruit production, whereas in *S. mauritianum*, where fruits were confined to terminal branched corymbs, only about 20% of the total canopy area was involved in fruit production. Five 0.25-m^2 quadrats were placed over the top of shrub branch at the positions marked by the labelled tags on the fruiting branches of each shrub, and the numbers of whole fruits present within each quadrat recorded at the commencement and again at the termination of the 30-day monitoring period. In *S. mauritianum*, the numbers of partly (25%, 50%, 75%) consumed fruits remaining in the corymbs after the 30-day monitoring interval were also recorded. Abscised fruits lost from the tagged branches of each shrub over the 30-day monitoring interval were collected in five 0.29-m^2 traps (within a recommended trap size for sampling seed rain in trees; Wiese, Zasada & Strong, 1998) placed beneath the tagged fruiting branches. Such trap sizes provide a representative seed rain measurement with negligible effect of mesh cover to prevent other some fruits from entering the trap. Each trap comprised of a 0.64 m long × 0.45 m wide × 0.18 m high collecting box clad with 1-cm-diameter wire mesh to allow fruit passage but prevent fruit predation by rodents (Mokotjomela & Hoffmann, 2013). Thus, the difference between the total numbers of fruits present in the canopy at the commencement of the study minus those present in the fruit traps plus those remaining in the plant canopy at the end of the study represented bird removal (Sallabanks, 1993; Korine, Kalko & Herre, 2000). A total of 80 records of seed removal (five records per fruiting species per site) were obtained over the 30-day monitoring period.

Daily seed removal rates (DSR) per shrub were computed from the following formula:

$$DSR = \{[(Ft_1 - (Ft_2 + AF)) \times 4]/30\} \times SF \times FCA \qquad (1)$$

where: Ft_1 = numbers of whole fruits at commencement of monitoring,

Ft_2 = numbers of whole and partial fruits at termination of monitoring,

AF = numbers of abscised fruits,

4 = conversion factor to m^2,

30 = monitoring interval in days,

SF = average numbers of seeds per whole or partial fruit,

FCA = fruiting canopy area m^2.

Chrysanthemoides monilifera, *O. africana* and *L. camara* fruits contained single seeds, whereas those of *S. mauritianum* contained an average of 66 ± 3 seeds per fruit. This was derived from subsamples of 50 fruits sampled at random from *S. mauritianum* shrubs at each study site.

Videographic technique

A digital camcorder (Kodak C813: 8.2 megapixel, ISO 1250, digital IS) provided permanent videographic records of the numbers of whole or partial fruits consumed by different species of birds over specific time intervals. Camcorder surveillances were conducted approximately 30 m distance from randomly selected individual reproductively mature alien and indigenous fruiting shrubs at each site. Surveillances were conducted during early morning (3-h period after sunrise) and late afternoon (3-h period before sunset) periods of peak bird activity over a 5-day monitoring period when the alien and indigenous shrub species were in full fruit (McNamara, Houston & Lima, 1994; Bibby *et al.*, 2000). From the total 480 h of surveillance (30 h per fruiting species per site), 192 h of actual bird foraging activity (about 12 h of actual bird foraging activity per fruiting species per site) were recorded with the camcorder. From the camcorder records, the total foraging periods in seconds spent by individual birds per day on each shrub species were documented. For the small single seed fruits of *C. monilifera*, *O. africana* and *L. camara*, all bird species consumed the entire fruit, that is, one seed per mouthful. For the large multiseed fruits of *S. mauritianum*, the fraction of the whole fruit removed by each bird species in one mouthful was estimated from its gape size. From the fractions of whole *S. mauritianum* fruits consumed, the numbers of seeds removed in one mouthful of fruit were determined from the average numbers of seeds present in each fruit. The total numbers of seeds removed by each bird species from each shrub per day (6-h observation period) were calculated from the product of the average numbers of seeds removed per second and the average foraging periods in seconds per day.

Statistical analyses

All measurements of seed removal rates which were spatial and temporally independent were $\log_e$-transformed before statistical analysis to reduce the inequality of variance in the raw data so these more closely approximated normal distributions. The experimental designs were unbalanced due to unequally replicated measurements. Consequently, a restricted maximum likelihood (REML) variance component analysis (linear mixed model) was applied to test for differences between the bird seed removal rates measured using the seed enumeration and videographic techniques from the indigenous and alien shrub species at the different sites and their interactions using the Wald X^2 statistic generated by the REML (GENSTAT Discovery Edition 3, VSL Lty, UK). Seed enumeration and videographic method, site and shrub species variables were fitted in the fixed model and method, site and shrub species factors in the random model. Differences exceeding twice the mean standard error of differences were used to separate significantly different treatment means at P 0.05. This was based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is two.

Results

There were no significant (P 0.05) differences in seed removal rates measured by the videographic and seed enumeration techniques between sites and shrub species with no significant (P 0.05) two-way and three-way interactions apparent between measuring approach, site and shrub species (Table 1). However, both the seed enumeration and the videographic techniques measured

Table 1 Wald χ^2 statistics derived from REML which tested for differences between seed enumeration and videographically measured seed removal rates by birds from alien (*Lantana camara* and *Solanum mauritianum*) and indigenous (*Chrysanthemoides monilifera* and *Olea europaea africana)* shrub species at different sites and their interactions

Fixed term	Wald χ^2 statistic	df	*P*
Method	0.08	1	0.783
Site	0.05	3	0.997
Shrub species	22.14	3	0.001
Method × Site	0.31	3	0.958
Method × Shrub species	0.44	3	0.932
Site × Shrub species	1.67	9	0.996
Method × Site × Shrub species	4.18	8	0.841

significantly (*P* 0.001) higher removal rates of seed by birds from the alien shrub *S. mauritianum* than the other alien and indigenous shrub species (Table 1; Fig. 1).

Discussion

The similar seed removal rates measured by the videographic and seed enumeration techniques between the single-seeded fruits of the alien and indigenous shrubs at each site supported the study hypothesis and pointed to relatively uniform daily fruit foraging intensities by the frugivorous birds over the peak fruiting periods of these shrubs. These relatively similar foraging rates by the frugivorous birds have been attributed to the low percentage of fruiting plants in the South African fynbos biome due to the presence of regular fires and large-scale clearing of indigenous forest for agricultural land use (Knight, 1988; Le Maitre & Midgley, 1992). In addition, whereas body size of different frugivorous bird species may dictate size of their seed loads (Jordano, 2000; Nathan *et al.*, 2008), the high frequency of foraging visitation by small birds possibly may have overridden the effect of body size on numbers of seeds removed. Indeed, the tiny *Z. pallidus* removed substantially larger numbers of the seeds from the multiseeded fruits of *S. mauritianum* than the other small species, *C. capensis* and the medium-sized birds (*C. striatus* and *T. olivaceous*), however not more than the large *C. arquatrix* (Fig. 2).

Studies have shown that high preference of *S. mauritianum* fruits in South African could be attributed to high sugar content and small seed matter (Jordaan *et al.*, 2011; Mokotjomela, Musil & Esler, 2013a). This finding was consistent with our hypothesis, and the reports indicating that Australian frugivorous birds preferentially dispersed alien fruits with few seeds but more sugar content in the pulp (Gosper & Vivian-Smith, 2010). Whereas provision of abundant *S. mauritianum* fruit resource for indig-

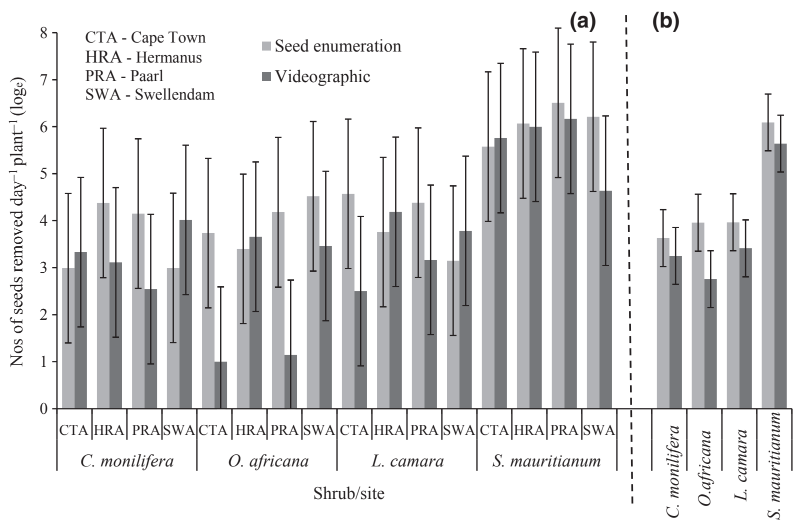

Fig 1 Average numbers of seeds removed per day by birds from the indigenous (*Chrysanthemoides monilifera* n = 58, and *Olea europaea africana* n = 27*)* and alien (*Lantana camara* n = 52, and *Solanum mauritianum* n = 61) shrubs at different sites derived from seed enumeration and videographic monitoring techniques (a). The bars to the right show the overall means of seed removal and standard errors, pooled over all sites for each of the species (b). Average standard error of differences shown by whiskers

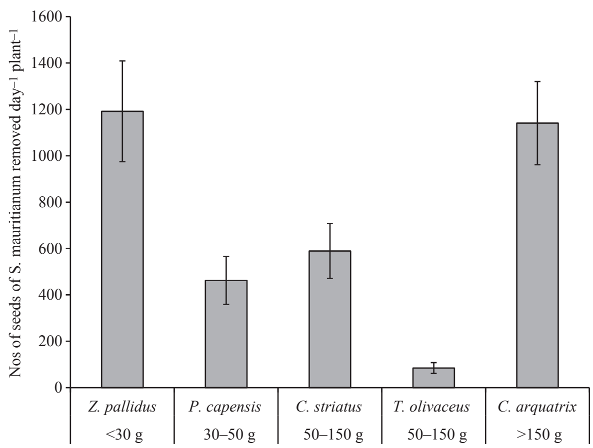

Fig 2 Average numbers of seeds of alien shrub *Solanum mauritianum* removed per day (measured by videographic method) by the tiny Cape white-eye (*Zosterops capensis*): n = 54, compared with those removed by the small Cape bulbul (*Pycnonotus capensis*): n = 31, the medium size olive thrush (*Turdus olivaceus*): n = 23, and speckled mousebird (*Colius striatus*): n = 17, and the large African olive-pigeon (*Columba arquatrix*) n = 12

enous birds and the fuelling of associated seed dispersal services are important for conserving local biodiversity (Mokotjomela *et al.*, 2009), the results also highlight a potential for further range expansion and invasion of pristine habitats. Consequently, management of alien plants in pristine habitats should prioritize eradication of seedlings especially where there is abundant perch material for birds.

Contrary to the study hypothesis, low preference of *L. camara* fruits by birds suggested that birds might not be primary dispersers. Consistently, porcupine droppings containing seeds were seen under *L. camara* thickets (Mokotjomela, 2012), and similar reports are known for Australia (Lawrie, 2002). Thus, other vertebrate vectors have important contribution in the dispersal of alien fleshy fruits as *L. camara* is ranked among 100 worst weeds of the word. We also attributed low preference of *L. camara* fruits to visual similarity of the fruits (e.g. dark black colour) to those of indigenous *C. monilefera* and *O. africana*. It has been shown that fruits of alien shrubs tend be preferential mostly in cases where they have different characteristics to those indigenous species thus suggesting indigenous species can compete given similar set of fruit characteristics (Aslan & Rejmánek, 2012).

There were several deficiencies associated with the seed enumeration technique that could potentially have affected fruit removal measurement accuracy. These included the inability of this technique to discriminate between asynchronous fruit production and fruit ripening in each shrub species (Knight, 1988; Korine, Kalko & Herre, 2000). For instance, presentation of fruits of mixed colour increases removal by birds and thus might explain causes of the difference rates of removal between shrubs (Willson & Thompson, 1982). The seed enumeration technique also did not discriminate between individual foraging bird species as well as contamination of fruit traps by wind-blown fruits abscised from neighbouring branches (Stevenson & Vargas, 2008) and fruit consumption by other fruit foraging organisms, specifically rodents and baboons, both from the tree plant canopy and from the fruit traps (Mokotjomela & Hoffmann, 2013). Such extraneous seed consumers have important contribution in net seed dispersal effectiveness of pertinent plant species and their population persistence (Dennis & Westcott, 2006; Godinez-Alvarez & Jordano, 2007). In this regard, Mokotjomela (2012) reported daily seed removal rates by rodents and other dispersal vectors from open-fruit traps of 250.2 ± 52.7 seeds in *S. mauritianum*, 3.4 ± 0.8 seeds in *C. monilifera* and 11.3 ± 1.4 seeds in *O. africana*, these comprising 40.4%, 4.6% and 12.6%, respectively of the daily seed removal rates by foraging birds. Consumption of fruits/seeds by nonstandard vectors (Higgins, Nathan & Cain, 2003) also includes frugivorous reptiles that disperse seeds as reported in South Africa (Whiting & Greeff, 1997) and the Canary Islands (Nogales, Delgado & Medina, 1998) as well as larval forms of invertebrates that damage seeds in the traps as reported in Columbia (Parrado-Rosselli, 2005).

In contrast, the videographic technique had several advantages in that it provided a detailed permanent videographic record of individual foraging bird species, their abundance and times they spent actively foraging on fruits as well as the quantities of whole or partial fruits and associated seeds consumed and other behavioural foraging traits (Korine, Kalko & Herre, 2000; Spiegel & Nathan, 2007; Prasad, Pittet & Sukumar, 2010; Kays *et al.*, 2011). Such information could potentially be incorporated into seed dispersal analytical models (Russo, Portnoy & Augspurger, 2006; Schurr *et al.*, 2009; Mokotjomela *et al.*, 2013c). The videographic technique allows identification of keystone seed dispersal vectors for specific plant species both birds and other organisms (Mokotjomela & Hoffmann, 2013) and thus assist in management decisions to limit the spread of invasive alien plants (Richardson & Rejmánek, 2011; Mokotjomela *et al.*, 2013c; Mokotjomela

& Hoffmann, 2013). We have shown that frugivorous bird species in the South African Mediterranean climate region tend to concentrate their foraging activity on an alien plant with abundant and nutritious fruit resources (Mokotjomela, Musil & Esler, 2013a), thereby supporting a proposal that animal–plant interactions assist in maintaining the dynamic equilibrium between plants and the environment (Garcia-Cervigon *et al.*, 2013). The findings of this study justify a proposal that future studies should consider using videographic techniques over seed enumeration techniques to increase precision of data, and number of studies on avian seed dispersal removal.

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