

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/237973903>

Frugivory by Taiwan Barbets (*Megalaima nuchalis*) and the effects of deinhibition and scarification on seed...

Article in *Canadian Journal of Zoology* · April 2012

DOI: 10.1139/z2012-030

CITATIONS

3

READS

61

4 authors, including:



Yafu Lee

National Cheng Kung University

35 PUBLICATIONS 269 CITATIONS

SEE PROFILE



Chen Jia-Huei

1 PUBLICATION 3 CITATIONS

SEE PROFILE

Frugivory by Taiwan Barbets (*Megalaima nuchalis*) and the effects of deinhibition and scarification on seed germination

Sing-Yi Chang, Ya-Fu Lee, Yen-Min Kuo, and Jia-Huei Chen

Abstract: We investigated the frugivory of Taiwan Barbets (*Megalaima nuchalis* Gould, 1863) on passage time and germination of 19 species of commonly consumed fruits, distinguished the deinhibition and scarification effects, and tested if complete bird-gut passage increases seed germination. We measured fruit and seed size and seed retention times (SRTs) and examined the germination of intact fruits and pulp-removed and defecated seeds. Germination latency in intact fruits of most species was prolonged, whereas in more non-figs (7/12), the seed germinability increased after ingestion, and nearly all figs germinated by higher proportions after defecation or depulping. Yet, figs revealed major differences from non-figs. SRTs of both non-figs and figs were negatively dependent on fruit size, which was positively correlated to seed size in non-figs only. The germinability was negatively correlated and the germination onset time was positively correlated with SRTs of the last seeds in non-figs, but neither was correlated with SRTs in figs. Most (14/17) species with germination success were enhanced either by deinhibition and scarification, or the fruits hardly germinated but were aided by pulp removal. Deinhibition revealed greater effects than scarification in increasing the germinability and shortening latency, thus aiding, in particular, non-fig seeds with shorter SRTs or that are often culled during feeding.

Key words: barbets, deinhibition, frugivore, germination, *Megalaima nuchalis*, scarification, seed dispersal.

Résumé : Nous avons étudié la frugivorie du barbu de Formose (*Megalaima nuchalis* Gould, 1863) en ce qui concerne le temps de transit et la germination de 19 espèces de fruits couramment consommés, départagé les effets de la désinhibition et de la scarification et vérifié si le transit complet dans l'intestin de l'oiseau se traduit par une augmentation de la germination des graines. Nous avons mesuré la taille des fruits et des graines et les temps de rétention des graines (SRT) et examiné la germination de fruits intacts, de fruits dont la pulpe avait été retirée et de graines déféquées. Pour la plupart des espèces, la durée de la latence de germination était plus longue pour les fruits intacts, alors que, pour une majorité de fruits n'appartenant pas au groupe des figues (7/12), la germinabilité des graines augmentait après ingestion, et presque toutes les figues germaient en plus grandes proportions après défécation ou dépulpage. Cependant, d'importantes différences ont été observées entre les figues et les non-figues. Les SRT des deux groupes de fruits étaient négativement dépendants de la taille des fruits, qui montrait une corrélation positive à la taille des graines seulement pour les non-figues. La germinabilité présentait une corrélation négative et le début de la germination présentait une corrélation positive avec les SRT des dernières graines des non-figues, alors que pour les figues, ni l'une ni l'autre de ces variables n'était corrélée aux SRT. Pour la plupart (14/17) des espèces présentant un succès de germination, la désinhibition ou la scarification contribuait à accroître la germination, ou alors les fruits étaient à peine germés, mais étaient aidés par le dépulpage. La désinhibition s'est avérée plus efficace que la scarification pour accroître la germinabilité et réduire la durée de latence, aidant ainsi plus particulièrement les graines de non-figues caractérisées par des SRT plus courts ou qui sont souvent écartées avant l'ingestion.

Mots-clés : barbus, désinhibition, frugivore, germination, *Megalaima nuchalis*, scarification, dispersion des graines.

[Traduit par la Rédaction]

Introduction

Plants constitute a significant or the only food resource to omnivores and herbivores, which can be further categorized according to which part of a plant is mainly or frequently eaten, e.g., frugivores (i.e., fruit eaters; Howe and Westley

1988). In contrast to a negative effect generally implied from being consumed by animals, frugivory usually does not involve direct impacts on a plant itself, instead a frugivore may even aid in dispersal, germination, or both and in turn contribute to the life history of plants and their demography (Levey et al. 2002; Paulsen and Högestedt 2002). Hence, fru-

Received 24 October 2011. Accepted 21 February 2012. Published at www.nrcresearchpress.com/cjz on 27 April 2012.

S.-Y. Chang.* Institute of Biodiversity, National Cheng Kung University, Tainan 701, Taiwan.

Y.-F. Lee* and Y.-M. Kuo. Institute of Biodiversity, National Cheng Kung University, Tainan 701, Taiwan; Department of Life Sciences, National Cheng Kung University, Tainan 701, Taiwan.

J.-H. Chen. Department of Life Sciences, National Cheng Kung University, Tainan 701, Taiwan.

Corresponding author: Ya-Fu Lee (e-mail: yafulee@mail.ncku.edu.tw).

*These authors contributed equally to this work.

givory and subsequent seed dispersal represent an intriguing plant–animal interaction that is implicitly connected to population dynamics and community composition of plants (Howe and Miriti 2004) and may be evident in the tropics where frugivorous seed dispersers are eminently documented (Primack and Corlett 2005).

Nonetheless, not every frugivore is an effective seed disperser, or at least not to every species of fruit consumed (e.g., Bradford and Westcott 2011). The number of visits made by a forager, the quantity of seeds taken from the parent plant, the sites where seeds are deposited, and the effects of ingestion and gut processing of a frugivore on seeds need to be examined when evaluating a frugivore's effectiveness in seed dispersal and contribution to a plant (Schupp 1993; Schupp et al. 2010). For instance, depending on whether seeds remain intact during ingestion and digestion of a fruit, some major frugivores such as pigeons and doves (Lambert 1989a; Primack and Corlett 2005) and parrots (e.g., *Amazona* spp.; Renton 2001; Shanahan et al. 2001) are actually seed predators.

The gut passage time of a frugivore often plays a role in effective dispersal, but in complex ways (Tewksbury et al. 2008). Long retention times may cause a higher chance of seed destruction, whereas a short retention time may leave seeds mostly unprocessed or defecated near a parent tree and thus with a lowered germination (Tewksbury et al. 2008) or reduced survival odds either before or after germination (Schupp 1993) due to density or distance-dependent predation and pathogen effects (i.e., the Janzen–Connell hypothesis; Clark and Clark 1984; but see Hyatt et al. 2003). Frugivores have diverse gut retention times, and the same frugivore may have different excretion patterns when processing different fruits (e.g., Fukui 2003). In the gizzard of a frugivorous bird, for instance, larger seeds may be more easily and generally quickly separated from the pulp (Levey and Duke 1992), although not necessarily true in all cases; thus fruits with larger seeds tend to have shorter seed retention times (SRTs) than those with smaller seeds (Levey and Grajal 1991; Fukui 2003; also see a review in Traveset 1998).

Effective seed dispersal also requires that a frugivore defecates the seeds intact in a viable condition, often a distance from the parent tree, and increases the chances of seed germination (Mayer and Poljakoff-Mayber 1989; Traveset 1998; Traveset and Verdú 2002; Linnebjerg et al. 2009; Schupp et al. 2010). The latter can be achieved by (i) a deinhibition process (Robertson et al. 2006) in which ingestion, digestion, or both separate seeds from the pericarp, which may contain inhibitors (e.g., in Japanese Rowan (*Sorbus commixta* Hedl.); Yagihashi et al. 1998), and (ii) scarification in which the digestion process scarifies the seed coat, promoting its permeability to water and gases (Traveset et al. 2008). Most previous studies, however, did not distinguish these two processes until recently (Samuels and Levey 2005; Robertson et al. 2006).

Barbets (Ramphastidae, Piciformes) are common tropical–subtropical birds and have been noted as primarily frugivorous in various areas, including southeastern Asia (Lambert 1989b), India (Yahya 2001), and Taiwan (Chen and Chou 2008). In fact, they are considered one of the most frugivorous birds and thus potentially important in seed dispersal, but they also are among the least studied birds in tropical

East Asia (Snow 1981; Corlett 1998; Shanahan et al. 2001). Previous studies on the barbet frugivory focused almost entirely on the diets or feeding behavior, with the effects of their ingestion and digestion on seed germination rarely examined (Snow 1981; Short and Horne 2001). We present the first study to specifically evaluate the potential role of frugivory by barbets in tropical East Asian forests by examining seed retention times and the effects of ingestion on seed germination. We tested the hypothesis that the retention time in a frugivore's gut is affected by morphological traits of the fruits and seeds (Levey and Duke 1992) and predicted that fruit species with larger seeds or lower pulp proportions would have shorter SRTs. For the effects of deinhibition and scarification (Traveset et al. 2008), we tested the hypothesis that digestion through a barbet's gut enhances seed germination and, specifically, predicted that scarification due to gut passage should result in an elevated chance of seed germination compared with depulping.

Materials and methods

The Taiwan Barbet (*Megalaima nuchalis* Gould, 1863) is an endemic species common in suburban woodlands, urban parks, and forests from lowlands to midelevation mountains (Brazil 2009). Fieldwork took place in the Hengchun Tropical Botanical Garden (HTBG) and the Guijiaou Experimental Forest (GEF; 120°48'E, 20°58'N, ca. 200–300 m in elevation and 450 ha in area) in Kenting, Taiwan, where the largest intact lowland monsoon reef–karst forest islandwide remains. Based on field observations of barbet foraging and plant phenology, we collected fruits of 19 species, with each species from at least three widely separated trees, of 12 families (Table 1). We measured the fruit and seed sizes and pulp proportions and water content of fruits for each species. Additional fresh intact fruits were collected for feeding and germination experiments. Seven barbets were maintained in captivity, each kept in an individual cage (60 × 45 × 45 cm) in an aviary (5.8 × 5 × 4 m). We provided water and fresh fruit supplemented daily with mealworms and followed the guidelines for the treatment of animals in behavioral research (Sherwin 2006).

Captive feeding sessions and subsequent seed germination experiments were conducted from August 2007 to March 2009. Each feeding session began at 0700, and from one to six barbets (2.1 ± 0.2 (mean \pm standard error (SE)) barbets per session) were used depending on the fruit supply and available manpower. In each session, we provided each barbet with 25 randomly chosen fruits of a particular species. A piece of paper (60 × 45 cm in size, marked off in 12 grids of 15 × 15 cm) was positioned in advance on the plate under the cage to collect defecated or regurgitated seeds and culled seeds from barbets handling the fruit. Observers remained in a separate space blocked by a board and curtain to avoid disturbing the barbets. The times when a fruit was picked up and then swallowed were recorded, thus measuring handling time. We noted the location and time of each dropping produced as precisely as possible, which often lasted for varying lengths of time and occurred before the last fruit ingestion. A session ended at least an hour after a barbet had taken its last fruit and 30 min after it stopped defecating. Seeds in drop-

Table 1. Fruit types of the plants tested, the fruit size (length \times width) and respective seed length (mean \pm SE; $n = 30$), water content, and pulp mass proportion (for non-fig species only).

Species* (family)	Fruit size (mm)	Seed length (mm)	Water content (%)	Pulp proportion (%)
<i>Ardisia sieboldii</i> ^{2,b} (Myrsinaceae)	0.9 \times 7.3	4.8 \pm 0.1	67.2 \pm 0.7	53.0 \pm 1.2
<i>A. squamulosa</i> ^{2,a,b}	6.8 \times 6.8	4.7 \pm 0.0	72.1 \pm 0.5	82.5 \pm 0.5
<i>Bischofia javanica</i> ¹ (Euphorbiaceae)	9.5 \times 11.0	4.3 \pm 0.1	65.9 \pm 1.2	89.4 \pm 0.2
<i>Champereia manillana</i> ² (Opiliaceae)	11.4 \times 9.9	9.5 \pm 0.4	68.8 \pm 0.7	65.3 \pm 1.6
<i>Diospyros ferrea</i> ^{2,b,c} (Ebenaceae)	13.9 \times 9.6	8.7 \pm 0.2	63.7 \pm 0.7	13.9 \pm 1.1
<i>Ehretia acuminata</i> ^{2,c} (Boraginaceae)	4.0 \times 4.7	2.9 \pm 0.0	70.9 \pm 0.7	68.0 \pm 3.3
<i>Leea guineensis</i> ^{1,b,c} (Leeaceae)	7.5 \times 11.8	4.1 \pm 0.1	76.7 \pm 0.8	74.3 \pm 1.3
<i>Machilus japonica</i> ^{2,b,c} (Lauraceae)	10.5 \times 11.4	10.3 \pm 0.2	45.0 \pm 0.6	37.6 \pm 1.3
<i>Myrica adenophora</i> ^{2,b} (Myricaceae)	9.4 \times 9.8	7.2 \pm 0.2	81.4 \pm 0.7	88.7 \pm 0.5
<i>Ptychosperma angustifolia</i> ^{2,a,c} (Arecaceae)	11.2 \times 9.3	10.0 \pm 0.2	57.5 \pm 0.8	58.9 \pm 0.8
<i>Trema orientalis</i> ² (Ulmaceae)	3.6 \times 3.3	2.0 \pm 0.0	56.1 \pm 2.2	88.7 \pm 0.7
<i>Viburnum odoratissimum</i> ^{2,b} (Caprifoliaceae)	11.5 \times 8.8	8.2 \pm 0.4	78.9 \pm 0.7	86.8 \pm 1.0
<i>Ficus ampelas</i> ³ (Moraceae)	7.2 \times 8.9	<1	76.0 \pm 0.6	—
<i>F. benjamina</i>	10.3 \times 9.2	<1	76.0 \pm 0.3	—
<i>F. caulocarpa</i>	7.2 \times 8.3	<1	74.8 \pm 1.6	—
<i>F. irisana</i>	12.2 \times 14.3	<1	82.8 \pm 0.3	—
<i>F. microcarpa</i>	9.0 \times 7.5	<1	71.4 \pm 0.6	—
<i>F. superba</i>	11.8 \times 13.8	<1	78.8 \pm 0.4	—
<i>F. virgata</i>	10.6 \times 11.4	<1	81.4 \pm 0.5	—

*Fruit types: 1, berry; 2, drupe; 3, fig (syconium). *a*, Species that are nonnative; *b*, species that are not a tree but a shrub; *c*, seeds that barbets had partially or fully regurgitated.

pings and regurgitated and culled seeds were collected and prepared for later germination experiments.

We prepared seeds for the germination experiments initially in four different groups: defecated seeds, regurgitated seeds, dropped seeds, and fresh intact fruits. The first three groups represent seeds retrieved after a specific feeding stage, but they could not be applied to all species tested due to differences in fruit characteristics. Seeds from regurgitation occurred only occasionally and in only a few species, so they were pooled with those of defecation in subsequent analyses. Dropped seeds were observed in even fewer instances, so we adopted pulp removal to mimic seeds that were culled from fruits by a barbet. Only the 12 non-fig species were used for the intact-fruit group, because there was no or extremely low germination of intact figs (also see [Lisci and Pacini 1994](#); [Otani and Shibata 2000](#); [Heer et al. 2010](#)).

For germination trials, at least three replicates were done for each plant species, each with seeds retrieved from a different feeding session. In each trial, we prepared 25 seeds or fruits (retrieved, depulped, or intact) for each treatment group of non-fig species, but 100 seeds were prepared for retrieved and depulped groups of fig species. Fig seeds were randomly picked with the aid of a microscope (10 \times 23 magnification, Zeiss Stemi 2000-C). We sowed seeds in cultivated soil mixed with lightweight expanded clay aggregate (LECA) and perlite in a proportion of 4:1:1 in pots, with each pot (25 \times 20 \times 7 cm) containing seeds from one experimental session of one fruit species; seeds were spaced \sim 1–2 cm apart. Most seeds were sowed 1 cm deep in the soil, but for tiny seeds of figs and those of *Ehretia acuminata* R. Br. and *Trema orientalis* (L.) Blume, seeds were placed on the soil surface for better tracking ([Baskin and Baskin 2001](#)). Pots were covered with a punctured limp plastic film to prevent water overevaporation and were kept in an outdoor environ-

ment with natural light and temperature. We watered the soil in a timely manner and checked daily for seed germination, which was defined as the emergence of any seedling part from the seed ([Izhaki et al. 1995](#)). Monitoring for each germination trial continued until all seeds had germinated, or for at least 12 months and if no seedling had emerged for at least a month since the last seedling emergence ([Traveset et al. 2001](#)). In two species, *Myrica adenophora* Hance and *Viburnum odoratissimum* Ker-Gawl., our monitoring lasted for over 18 months. Most nongerminated seeds in the latter condition, particularly those of figs, were found nonvital due to fungus infection or rotten from unknown causes.

Data are presented as mean \pm standard error (SE), unless otherwise noted. We used STATISTICA 6.0 (StatSoft Inc. 2001) for all statistical analyses. In the feeding experiments, we calculated seed retention time (SRT) for each species as the difference between the times of defecation and ingestion. This was possible for fruits with large-sized seeds, where defecation came after an ingestion of a single fruit, or for small-seed fruits that were ingested in bouts of short periods (2.77 \pm 0.29 min, $n = 54$). For other small-seed fruits that were taken irregularly and defecation came before the last fruits, we assumed that seeds were defecated in the order in which the fruits were ingested ([Murphy et al. 1993](#)). We distinguished SRTs as the first (time elapsed until the first defecated seed appeared; FSRT), the last (time elapsed until the final seed was defecated; LSRT), and the mean (when all or most of the seeds were recovered) or the median (the averaged time between the first and last SRTs; MSRT). In the germination experiments, we calculated germinability as the proportion of seeds germinated of the total seeds sowed and measured the latency to germination to describe germination speed, including the onset of germination (T_0 ; the time until the first seed germinated) ([Barnea et al. 1991](#); [Traveset et al.](#)

2001) and the mean length of time elapsed (T_m) (Ranal and Santana 2006). We used a stepwise regression to determine relationships between SRTs and morphometric traits (fruit length and width and seed size, water content, and pulp percentage) and examined relationships among morphometric characteristics of fruits by a Pearson correlation coefficient (r). Our field observations of barbet feeding allowed comparisons of the mean postfeeding stay duration of barbets on a tree with the SRT obtained in the feeding experiments to evaluate the probability of seed dispersal by barbets.

Differences among treatments for each fruit species were examined using analysis of variance (ANOVA) and subsequent post hoc comparisons by Tukey's honest significant difference (HSD). All data were first assessed for the homogeneity in variance by Levene's test (for two-group comparisons) or Bartlett's test (for three-group comparisons). Proportional data were arcsine (square root) transformed, and the data of germination latency and duration were logarithmically transformed to meet the criteria of normality (Zar 1999). In a few cases in which the normality of the data could not be achieved by transformation, they were examined by the Mann-Whitney U test (for two groups) or the Kruskal-Wallis test (for three groups) followed by the Nemenyi test for post hoc comparisons (Zar 1999).

We compared the germination of seeds from which the pulp had been removed with that of seeds of intact fruits to evaluate the effect of deinhhibition and the germination of the former with that of seeds that had been defecated to evaluate the effect of scarification (Samuels and Levey 2005). We used the natural log of the odds ratio ($\ln OR$) to calculate the sizes of the deinhhibition and scarification effects on germinability (Traveset and Verdú 2002), where $OR = p_1(1 - p_2)/p_2(1 - p_1)$ (Cooper and Hedges 1994). In examining the deinhhibition effect, p_1 and p_2 represented the proportion of germination of depulped seeds and that of intact fruits, respectively, whereas for the scarification effect, p_1 and p_2 referred to the germinability of digested and depulped seeds, respectively. When a p value was 0% or 100%, $\ln OR$ became infinite and meaningless; thus we substituted the respective readings with 0.05% and 99.95% to make an estimation possible (Robertson et al. 2006). A positive $\ln OR$ value indicated an enhancing effect, whereas a negative value indicated an inhibitory effect on germination. Differences in T_0 among treatments (ΔT_0) were further adopted to estimate the inhibition and scarification effects on germination speed; a negative value indicated shortened germination arrest, and a positive value indicated prolonged latency. We used a t test to compare differences between the inhibition and scarification effects of $\ln OR$ and ΔT_0 and used χ^2 to examine if the proportions of $\ln OR$ and ΔT_0 between treatments were independent of fruit species.

Results

SRTs and morphometric traits of fruits

We completed 58 sessions of feeding experiments in which barbets consumed a total of 3378 fruits of 19 species. Seeds of *Machilus japonica* Sieb. & Zucc. var. *kusanoi* (Hayata) Liao were regurgitated exclusively; those of *Champereaia manillana* (Bl.) Merr., *Diospyros ferrea* (Willd.) Bakhuizen, *Leea guineensis* G. Don, and *Ptychosperma angustifolium*

Blume came from both defecation and regurgitation; and those of the other 14 species were all retrieved from defecation. Fruit species that were either fully or partially regurgitated were greater in fruit length (10.91 ± 1.03 mm; $t_{[10]} = -2.29$, $p < 0.05$), width (10.39 ± 0.5 mm; $t_{[10]} = -2.30$, $p < 0.05$), and seed size (8.53 ± 1.15 mm; $t_{[10]} = -2.66$, $p < 0.05$) but had a lower pulp proportion ($50.0\% \pm 10.86\%$; $t_{[10]} = 2.69$, $p < 0.05$) compared with those with seeds that were excreted exclusively (fruit length, 7.25 ± 1.13 mm; fruit width, 7.37 ± 1.04 mm; seed length, 4.86 ± 0.83 mm; pulp proportion, $79.59\% \pm 5.26\%$; Table 1).

The mean FSRT (16.6 ± 1.6 min, range = ~9–29 min; Kruskal-Wallis test, $F_{[17,107]} = 37.69$, $p < 0.005$), MSRT (26.9 ± 1.9 min, range = ~15–48 min; $F_{[17,84]} = 3.64$, $p < 0.001$), and LSRT (36.0 ± 3.1 min, range = ~15–66 min; $F_{[17,85]} = 2.88$, $p < 0.001$) varied among species (Table 2). *Trema orientalis* had the longest mean SRTs among the 19 species. Several fig species (e.g., *Ficus benjamina*, *F. microcarpa*, *F. ampelas*, and *F. virgate*) followed, especially in MSRT (of >29 min) and LSRT (of >40 min). FSRTs of neither non-figs ($R^2 = 0.35$, $F_{[2,9]} = 3.99$, $p > 0.05$) nor figs ($R^2 = 0.44$, $F_{[1,3]} = 5.68$, $p > 0.05$) were dependent on fruit traits. MSRTs of non-figs, however, were dependent on fruit width ($R^2 = 0.67$, $F_{[1,9]} = 21.07$, $p < 0.001$; MSRT = $49.1 - 2.87 \times$ fruit width), whereas LSRTs of both non-figs ($R^2 = 0.74$, $F_{[1,9]} = 29.57$, $p < 0.001$; LSRT = $70.27 - 4.61 \times$ fruit length) and figs ($R^2 = 0.66$, $F_{[2,4]} = 6.92$, $p < 0.05$; LSRT = $56.33 - 5.4 \times$ fruit width, $p < 0.05$) were dependent on fruit size. Yet, fruit length ($r = 0.87$, $p < 0.001$) and width ($r = 0.6$, $p < 0.05$) were both correlated with seed size for non-figs. SRTs of most species were longer than the lengths of the postfeeding stay duration of barbets, except those of *F. superba* and *L. guineensis* (Table 2).

Germinability and germination speed

During the 196 germination trials (125 for non-figs and 71 for figs), all species exhibited varying degrees of germinability in different treatments (Figs. 1a and 1b), but *M. adonophora* and *V. odoratissimum* did not germinate in any treatment. In non-figs, *C. manillana* and *T. orientalis* barely germinated from intact fruits, less than 10% of *Bishofia javanica* Blume, *D. ferrea*, and *E. acuminata* did, whereas *Ardisia sieboldii* Miq., *A. squamulosa* Presl., and *P. angustifolium* reached ~70%–80%. In contrast, all 10 species in the defecated-regurgitated (~44.5%–100%) and depulped (~33.3%–94.7%) groups germinated. *Bishofia javanica*, *D. ferrea*, *E. acuminata*, *L. guineensis*, *M. japonica*, and *T. orientalis* all had lower germinability of intact fruits than in the other treatments, whereas germinability of *P. angustifolium* was higher in the defecated-regurgitated group than in the depulped group (Fig. 1a). The figs all germinated in the defecated and depulped treatments by different proportions (~45.8%–97%), but almost none from intact fruits; the germinability of *F. superba* was significantly lower in the defecated group than in the depulped group ($H_{[6,35]} = 19.54$, $p < 0.05$; Fig. 1b).

The time to germination differed among species and among treatment, but seeds in intact fruits of most species revealed a prolonged germination latency (Fig. 2). Germination onset (T_0 = ~26–127 days) began later and mean latency (T_m = ~26–140.7 days) lasted longer in intact non-figs than

Table 2. Seed retention times (SRTs; FSRT, MSRT, and LSRT; mean \pm SE) of each plant species (n = replicated sample sizes) and postfeeding stay duration (PFSD; n = observations) of Taiwan Barbets (*Megalaima nuchalis*) on trees.

Species	FSRT	MSRT	LSRT	PFSD
<i>A. sieboldii</i> (3)	9.2 \pm 2.0	26.3 \pm 9.6	40.1 \pm 19.4	2.0 \pm 1.4 (6)
<i>A. squamulosa</i> (5)	16.5 \pm 2.0	27.0 \pm 3.1	33.7 \pm 7.4	0.2 \pm 0.2 (2)
<i>B. javanica</i> (5)	11.4 \pm 1.9	18.3 \pm 1.8	22.8 \pm 3.4	5.0 \pm 2.5 (31)
<i>C. manillana</i> (3)	26.8 \pm 2.6	28.2 \pm 0.1	27.9 \pm 2.3	2.5 \pm 1.0 (15)
<i>D. ferrea</i> (5)	12.0 \pm 3.6	19.0 \pm 2.3	23.5 \pm 5.2	0.2 \pm 0.1 (18)
<i>E. acuminata</i> (3)	17.3 \pm 10.6	27.9 \pm 11.2	36.6 \pm 14.8	1.2 \pm 0.8 (23)
<i>L. guineensis</i> (3)	17.2 \pm 1.9	14.5 \pm 3.5	15.2 \pm 5.0	32.7 \pm 11.7 (16)
<i>M. japonica</i> (9)	4.6 \pm 1.6	—	—	0.3 \pm 0.2 (42)
<i>M. adenophora</i> (3)	18.8 \pm 4.6	24.3 \pm 3.6	27.1 \pm 3.0	8.7 \pm 2.9 (7)
<i>P. angustifolia</i> (2)	15.8 \pm 0.2	17.4	19.2	3.0 \pm 2.2 (4)
<i>T. orientalis</i> (11)	28.8 \pm 3.0	48.1 \pm 3.4	65.9 \pm 7.5	1.6 \pm 0.6 (55)
<i>V. odoratissimum</i> (4)	12.3 \pm 4.9	24.4 \pm 7.7	36.5 \pm 11.0	0.9 \pm 0.5 (3)
<i>F. ampelas</i> (9)	10.6 \pm 1.3	30.0 \pm 3.1	47.3 \pm 6.3	0.8 \pm 0.4 (19)
<i>F. benjamina</i> (7)	20.7 \pm 4.7	36.9 \pm 7.0	51.9 \pm 11.4	0.5 \pm 0.4 (9)
<i>F. caulocarpa</i> (6)	12.0 \pm 1.0	23.6 \pm 3.6	35.2 \pm 7.9	1.3 \pm 0.9 (28)
<i>F. irisana</i> (7)	21.9 \pm 3.4	28.3 \pm 2.9	34.6 \pm 5.8	1.9 \pm 1.8 (5)
<i>F. microcarpa</i> (13)	15.8 \pm 2.2	36.8 \pm 3.7	57.0 \pm 6.9	0.2 \pm 0.1 (14)
<i>F. superba</i> (10)	15.1 \pm 1.3	23.5 \pm 1.9	31.2 \pm 3.7	15.0 \pm 6.2 (6)
<i>F. virgata</i> (9)	16.6 \pm 2.8	29.6 \pm 2.8	42.5 \pm 6.0	1.9 \pm 1.8 (10)

Note: Data of *Machilus japonica* refer to only times of regurgitation. Data of *Ptychosperma angustifolium* for MSRT and LSRT were available from only one replicate.

in both the defecated–regurgitated group (T_0 = ~8–56 days, T_m = ~11.5–81.5 days) and depulped group (T_0 = ~8–64 days; T_m = ~11.6–98.8 days). T_0 values of *A. sieboldii*, *D. ferrea*, *E. acuminata*, and *M. japonica* and T_m values of *A. sieboldii*, *B. javanica*, *E. acuminata*, *L. guineensis*, *M. japonica*, and *P. angustifolium* were longer in intact fruits than in the defecated, depulped, or both groups, whereas T_m values of *C. manillana*, *L. guineensis*, *P. angustifolium*, and *T. orientalis* were longer in the depulped group than in the defecated group (Figs. 2a and 2b). In figs, the T_0 of *F. benjamina* and the T_m of *F. microcarpa* were shorter in the defecated group than in the depulped group, but defecated *F. superba* and *F. irisana* seeds had greater T_0 and T_m values, respectively. Among species, the germinability was negatively (r = –0.76, p < 0.01), but the latency values were positively (T_0 , r = 0.78, p < 0.05; T_m , r = 0.73, p < 0.05), correlated with the LSRT in non-figs, whereas neither the germinability nor the latency to germination was correlated to SRTs in figs.

Deinhibition, scarification, and seed germination

The 17 species of fruits with successful germination can be categorized into four types based on the effect size (Fig. 3). Type I contained species that germinated from intact fruits and were only lightly affected by depulping and digestion, as exemplified by *A. sieboldii* and *A. squamulosa*. In type II, seeds of intact fruits did not or only slightly germinated but were aided by pulp removal and thus by a greater deinhibition effect. Species in type III had similar germination proportions in intact fruits and depulped groups, which were enhanced by gut passage and thus by a greater scarification effect, e.g., *Ptychosperma angustifolium*. In type IV, both deinhibition and scarification enhanced seed germinability of most species, except that of *F. superba* in which the

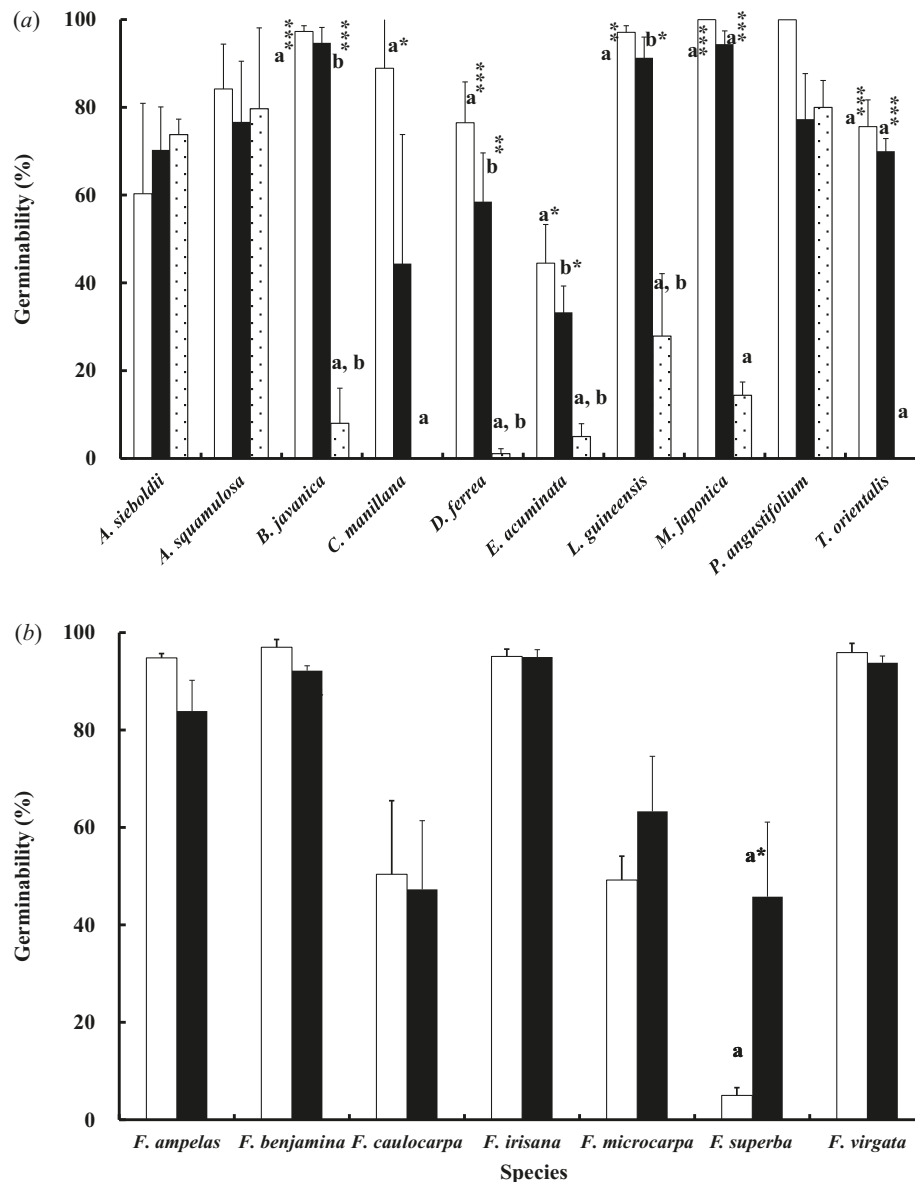
scarification effect lowered the germinability compared with that with deinhibition.

Effect sizes of scarification ($\ln \text{OR} = 0.97 \pm 0.5$, 95% CI = –0.09–2.02, with 64.7% of species possessing a $\ln \text{OR}$ value of ≤ 1) were significantly smaller than those of deinhibition ($\ln \text{OR} = 5.82 \pm 0.90$, 95% CI = 3.90–7.73, with 17.7% of species possessing a $\ln \text{OR}$ value of ≤ 1 ; $t_{[16]} = 4.16$, p < 0.01) in most species. The two effects, however, differed among species: deinhibition ($\chi^2_{[16]} = 38.19$, p < 0.01) and scarification ($\chi^2_{[16]} = 85.36$, p < 0.001) (Fig. 3a). The deinhibition effect sped up germination by 41.31 ± 12.22 days (range = ~2.4–133 days); in contrast, the scarification shortened germination latency by 3.8 ± 1.2 days (range = ~0.1–9.3 days) in some species, but prolonged it in others (6.3 ± 2.2 days, range = ~0.5–14.6 days) (Fig. 3b). The deinhibition process (ΔT_0 , -23.55 ± 8.54 , 95% CI = –38.5 to –8.6) had a greater overall effect in shortening germination latency than did scarification ($\Delta T_0 = 0.28 \pm 1.59$, 95% CI = –9.3 to 14.6; $t_{[9]} = -3.83$, p < 0.01).

Discussion

Seed retention times (SRTs) within a frugivore’s gut are the main correlate affecting the extent of germination (e.g., germinability; Traveset and Verdú 2002) and are generally considered to be negatively correlated with seed size (Levey and Grajal 1991; Fukui 2003; but for exceptions, see Wotton et al. 2008). Our data, although using an indirect relationship between seed size and fruit size, support the latter notion and confirm the prediction regarding pulp proportion. The medium or mean SRTs of Taiwan Barbets were approximately 15–45 min and concur with those previously reported for small- or medium-sized avian frugivores (e.g., Lambert 1989a; Fukui 1996; Linnebjerg et al. 2009). Yet, we also found support for the general conclusion of a negative corre-

Fig. 1. Mean (\pm SE) germinability of defecated (open bars) and pulp-removed (solid bars) seeds and intact fruit (dotted bars) of (a) 12 species of non-fig and (b) seven species of fig plants tested and showing germination. A letter and asterisks indicate a significant difference between a treatment group and another group with the same letter within each respective species. Only defecated and pulp-removed groups were presented for *Ficus* species because of no or extremely low germination over the study period. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.



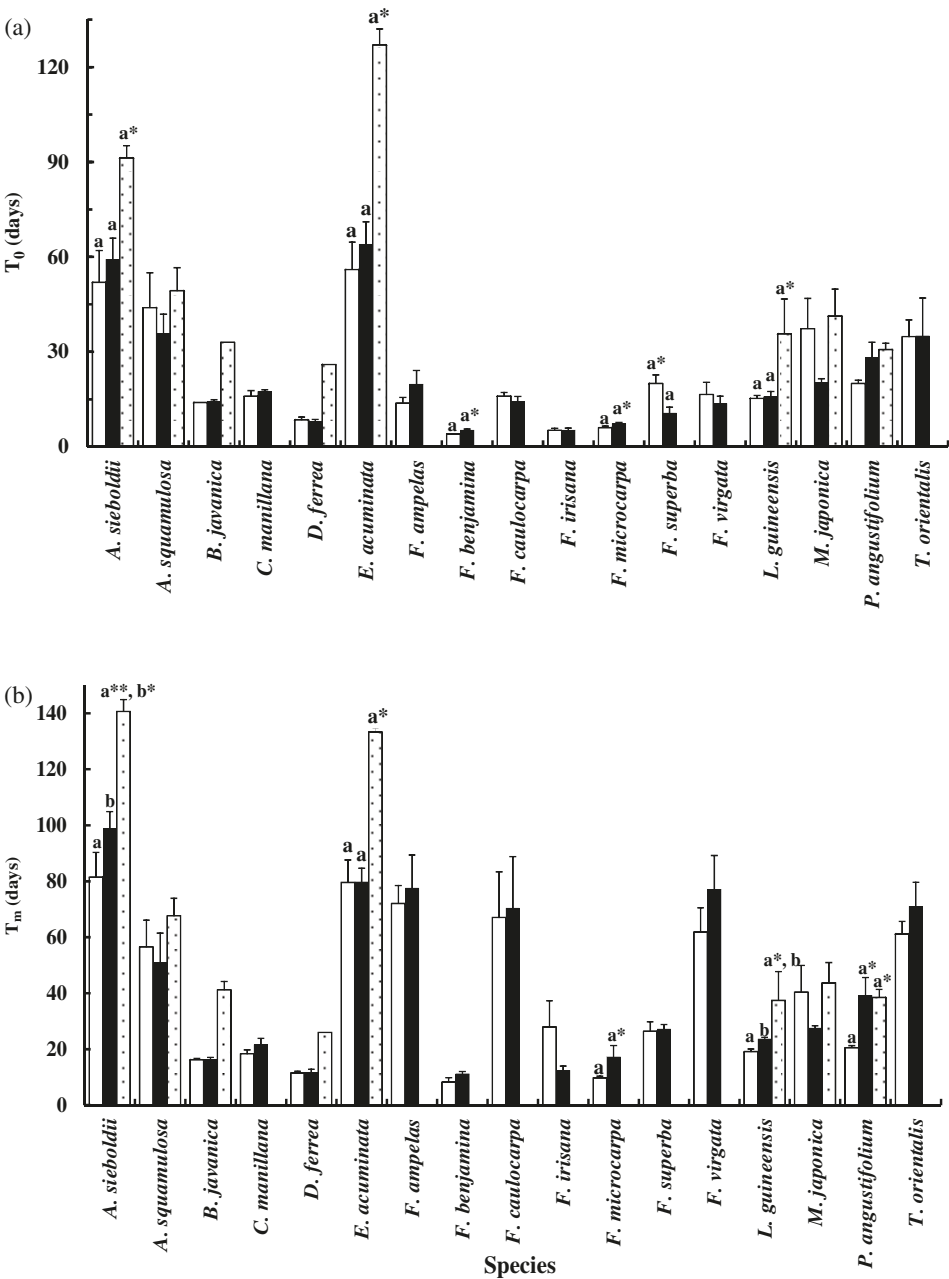
lation between retention time and germination success (Traveset and Verdú 2002) in the 12 non-fig species, but not for figs. Their relationships vary considerably among different species of fruits (e.g., Barnea et al. 1991; Murray et al. 1994; Tewksbury et al. 2008).

Our results indicate that frugivory by Taiwan Barbets, through gut passage or by seed regurgitation, enhances the seed germinability in eight of the 12 non-fig (66.7%) and all seven fig species. To the best of our knowledge, this is the first study to experimentally demonstrate the effects of fruit consumption on seed germination by a major frugivore in tropical East Asia. This and the fact that SRTs of 17 species (89.5%) tested were longer than the mean postfeeding stay duration of barbets on each respective plant species suggest that at least some seeds of most of the fruits ingested may

be carried away from the parent tree, and barbets play an effective seed dispersal role in forests of Kenting, tropical southern Taiwan.

Frugivory by Taiwan Barbets aided germination by both deinhibition and scarification processes, although both acted to different degrees and vary among species, evidenced by the four types of effect sizes illustrated in our study. Traveset (1998) noted that pulp removal is sufficient to accelerate germination percentages. Yet, the deinhibition process has not garnered sufficient attention when discussing the influences of digestion on seed germination. Most previous studies considered only the scarification effect in improving seed germination as they failed to test intact fruits (reviews in Samuels and Levey 2005; Robertson et al. 2006; Bradford and Westcott 2010). Our study distinguished the deinhibition effect

Fig. 2. Difference in (a) mean (\pm SE) germination latency in days after sowing (T_0) and (b) mean latency (T_m) among defecated (open bars) and pulp-removed (solid bars) seeds and intact fruits (dotted bars). A letter and asterisks indicate a significant difference between a treatment group and another group with the same letter within each respective species. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

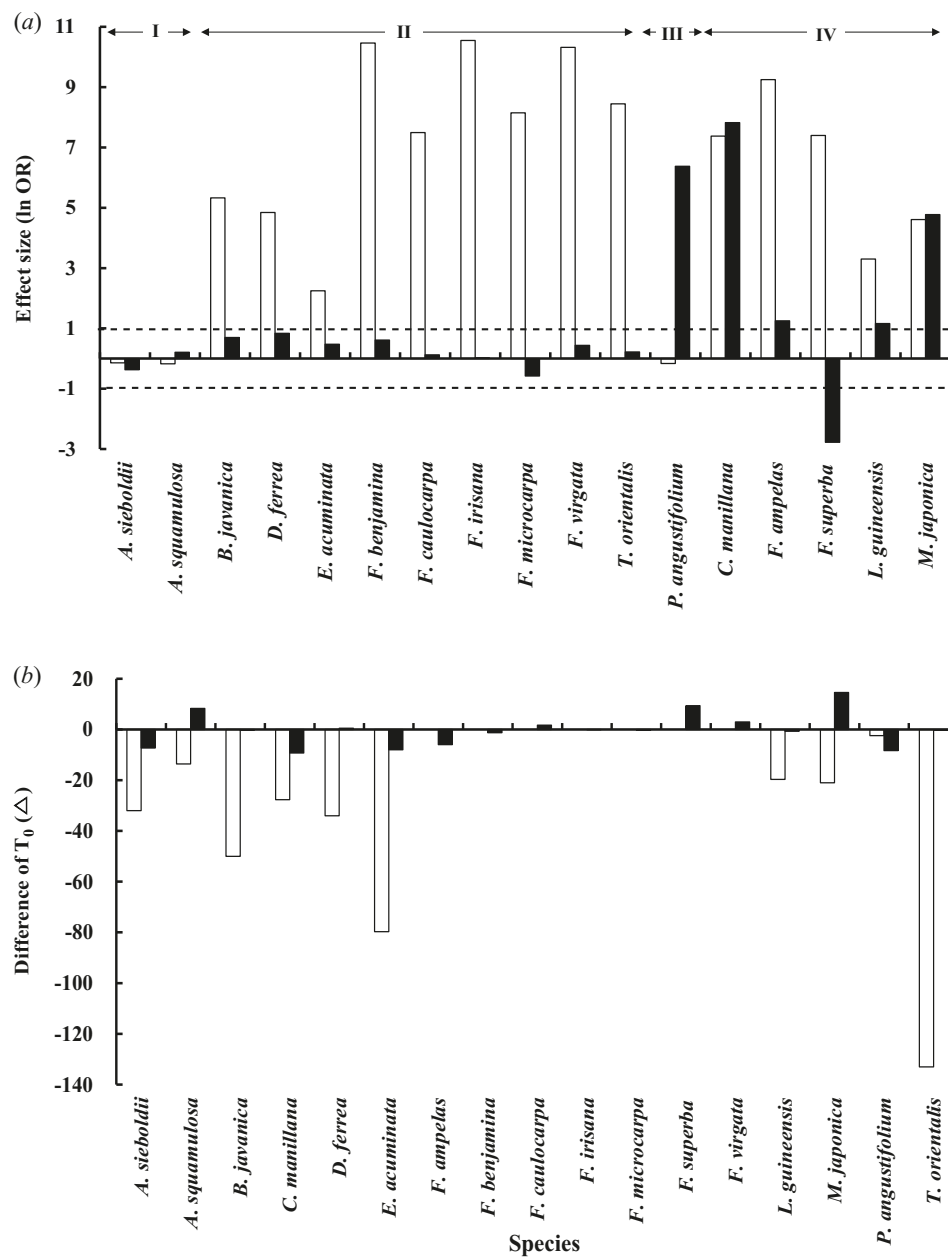


from the scarification effect for most of the species tested and showed that overall the former is a more important force in stimulating germination for over 75% of the species tested by the effect size of \ln ORI or by the degree of the shortening of latency, ΔT_0 . We found an even higher mean deinhibition effect than that concluded in Robertson et al. (2006), but the absolute value of ≤ 1 for the effect size of scarification in 11 of the 17 species tested (64.7%) is comparable with that concluded in Robertson et al. (2006). This contradicts our prediction and the general thought regarding the effect of de-inhibition relative to that of scarification.

Regurgitation is not uncommon in frugivorous birds (Sorensen 1984; Corlett 1998), yet it is rarely reported for barbets

(e.g., Godschalk 1985). We documented the first record of seed regurgitation, although only occasionally, by an East Asian barbet that is a gulper and will typically swallow a fruit whole if it is suitable for its gape size without culling. Seeds that were regurgitated usually went through a less complete digestion process and had shorter gut retention times, e.g., from ≤ 3 min (*L. guineensis*, *M. japonica*) to 19 min (*C. manillana*, this study); thus, in general, they would be more likely be discarded near the parent tree (Traveset et al. 2007), which applies to and will particularly be the case for culled seeds. This is also related to seed size, as species with regurgitated seeds tended to have larger seed sizes and lower pulp mass proportions, as predicted. In our study,

Fig. 3. (a) Effect sizes (ln OR) of deinhibition (open bars) and scarification (solid bars) and the (b) respective difference in the effect size (Δ) of deinhibition (open bars) and scarification (solid bars) effects on T_0 .



these include *D. ferrea*, *M. japonica*, and *P. angustifolia*. The germinability of these species can be increased through depulping if culled during feeding or by less complete gut passage followed by regurgitation. Their fate, however, will still be subject to confounding factors such as many or most of these seeds may fall near or directly underneath the parent tree (Clark and Clark 1984).

Fruit consumption by barbets, especially through the deinhibition, also advanced the onset of germination by varying degrees in most of the species tested for which comparable data from intact fruits were available. A difference in germination speed of a few days is not likely to result in an important effect to seedling survival (Traveset and Verdú 2002), yet we observed advances in the germination onset of up to months (e.g., *T. orientalis*, *B. javanica*, *E. acuminata*, and

figs). A much shortened time to germination may aid in the survival and establishment of seedling in seasonal environments with limiting physical conditions such as the lengthy dry season in Kenting, as well as in many other tropical-subtropical areas. Germination requires breaking the primary and secondary dormancy phases (Mayer and Poljakoff-Mayber 1989; Hilhorst 2007). Although the mechanisms for breaking secondary dormancy (e.g., metabolic blocks) are still not well understood, the primary dormancy can be regulated endogenously (morphologically or physiologically), exogenously (physical, mechanical, or chemical), or by a combination of the mechanisms (Nikolaeva 1977; Hilhorst 2007). Gut passage of seeds often breaks only exogenous controllers such as the seed coat and chemical inhibitors contained in fruit pulp. A delayed germination or dormancy may

be advantageous if it increases a seed's chance to survive harsh physical environmental conditions, but seeds may still suffer from predation and pathogen infections (Clark and Clark 1984).

Among the 12 species of non-figs tested, the germinability of seeds that had experienced gut passage or both gut passage and depulping significantly increased in eight species, but not so in *A. sieboldii*, *A. squamulosa*, *M. adenophora*, or *V. odoratissimum*. In both *Ardisia* species, passage through a barbet's gut still shortened the germination latency, but no seed germinated in any treatment for *M. adenophora* and *V. odoratissimum* over the first six months, when most other species had germinated by different proportions, and thereafter. Nikolaeva (1977) categorized *Myrica* as typical of both mechanically and physiologically controlled dormancy. Baskin et al. (2008) indicated that gibberellins or additional cold combined with warm-cold temperature stratification is required to break *V. odoratissimum*'s morphophysiological dormancy, or germination can barely be achieved. A similar pattern was observed in *M. rubra* (Chen et al. 2008), to which *M. adenophora* is closely related. Fukui (1995) also noted that after being treated with cold temperature (~0–5 °C) for 120 days before the experiments, 60% of *V. dilatatum* seeds defecated by Brown-eared Bulbuls (*Ixos amaurotis* Temminck, 1830) germinated.

No or extremely low proportions of germination in intact fruits were also noted in other fig species examined elsewhere (e.g., Lisci and Pacini 1994; Alves-Costa and Eterovick 2007; Bradford and Westcott 2010; Heer et al. 2010). Compared with depulped seeds, digestion by barbets decreased the germinability of *F. superba* from 45% to 5%. This was unique and not recorded for any other *Ficus* in this study, and we cannot offer explanations at the moment. Otani and Shibata (2000) found that no hand-cleaned seeds of *F. superba* germinated, but up to over 90% of those digested by Japanese macaques (*Macaca fuscata* Blyth, 1875) did. Within the same genus, different species of fruits may not display similar germination patterns (Otani and Shibata 2000) or respond to digestion processes in similar ways (Tewksbury et al. 2008). Even the same species may reveal different germination trends when growing in distinct areas or being digested by different animals (Traveset 1998).

Barbets in Kenting forests fed on 41 or more species of fruits; the 19 species tested by our study constituted over 87% of the fruit-feeding records, and the majority of these plants are native (S.Y. Chang and Y.F. Lee, unpublished data). Among the 17 species that exhibited germination success, 11 species (64.7%) either did not germinate from intact fruits or had low germinability (<10%) unless the pulp was removed. Ingestion by barbets and subsequent digestion can play significant roles that contribute to the dynamics of this reef-karst forest in tropical Taiwan. Although larger-sized frugivores often travel larger ranges (e.g., hornbills; Holbrook and Smith 2000), barbets may still fly relatively long distances. Yellow-crowned Barbets (*M. henricii* Temminck, 1831) fly up to 700 m, with a home range of 7.6 ha (Lambert 1989b). In tropical East Asia, seed dispersal distances range from 100 m to 1 km for small- to medium-sized forest passerines (Corlett 2009). Future studies to critically examine composite seed shadow patterns, incorporating the behavioral and movement patterns of frugivores and the relationships

with the seedling establishment (Westcott et al. 2005), within forests or across landscape matrix (Schupp et al. 2010), may further illuminate the implications of barbet frugivory for the tropical forest composition and long-term dynamics.

Acknowledgments

The Hengchun Research Center, Taiwan Forestry Research Institute, and the Forestry Bureau provided logistic support; the Taiwan Endemic Species Research Institute and the Noah Wetland Society and Rescue Center provided barbets for our experiments. G.N. Wang, S.H. Wu, C.L. Pan, and H. Y. Tzeng assisted in the field with phenology and fruit sampling. Our study was supported by the National Science Council, Taiwan (NSC: 97-2621-B-006-007).

References

- Alves-Costa, C.P., and Eterovick, P.C. 2007. Seed dispersal services by coatis (*Nasua nasua*, Procyonidae) and their redundancy with other frugivores in southeastern Brazil. *Acta Oecol.* **32**(1): 77–92. doi:10.1016/j.actao.2007.03.001.
- Barnea, A., Yom-Tov, Y., and Friedman, J. 1991. Does ingestion by birds affect seed germination? *Funct. Ecol.* **5**(3): 394–402. doi:10.2307/2389811.
- Baskin, C.C., and Baskin, J.M. 2001. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, Calif.
- Baskin, C.C., Chien, C.T., Chen, S.Y., and Baskin, J.M. 2008. Germination of *Viburnum odoratissimum* seeds: a new level of morphophysiological dormancy. *Seed Sci. Res.* **18**(3): 179–184. doi:10.1017/S0960258508042177.
- Bradford, M.G., and Westcott, D.A. 2010. Consequences of southern cassowary (*Casuarius casuarius*, L.) gut passage and deposition pattern on the germination of rainforest seeds. *Austral Ecol.* **35**(3): 325–333. doi:10.1111/j.1442-9993.2009.02041.x.
- Bradford, M.G., and Westcott, D.A. 2011. Predation of cassowary dispersed seeds: is the cassowary an effective disperser? *Integr. Zool.* **6**(3): 168–177. doi:10.1111/j.1749-4877.2011.00242.x. PMID:21910837.
- Brazil, M. 2009. Birds of east Asia. Princeton University Press, Princeton, N.J.
- Chen, C.C., and Chou, L.S. 2008. Differences in foraging ecology between generalized and specialized frugivorous birds in the Fushan Experimental Forest, Northern Taiwan. *Taiwan J. For. Sci.* **23**: 233–242.
- Chen, S.Y., Kuo, S.R., and Chien, C.T. 2008. Roles of gibberellins and abscisic acid in dormancy and germination of red bayberry (*Myrica rubra*) seeds. *Tree Physiol.* **28**(9): 1431–1439. doi:10.1093/treephys/28.9.1431. PMID:18595855.
- Clark, D.A., and Clark, D.B. 1984. Dynamics of a tropical rain forest tree: evaluation of the Janzen–Connell model. *Am. Nat.* **124**(6): 769–788. doi:10.1086/284316.
- Cooper, H., and Hedges, L.V. 1994. The handbook of research synthesis. Russell Sage Foundation, New York.
- Corlett, R.T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. *Biol. Rev. Camb. Philos. Soc.* **73**(4): 413–448. PMID:9951414.
- Corlett, R.T. 2009. Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica*, **41**(5): 592–598. doi:10.1111/j.1744-7429.2009.00503.x.
- Fukui, A. 1995. The role of the Brown-eared Bulbul *Hypsypetes amaurotis* as a seed dispersal agent. *Res. Popul. Ecol. (Kyoto)*, **37**(2): 211–218. doi:10.1007/BF02515822.
- Fukui, A. 1996. Retention time of seeds in bird guts: costs and

- benefits for fruiting plants and frugivorous birds. *Plant Species Biol.* **11**(2–3): 141–147. doi:10.1111/j.1442-1984.1996.tb00139.x.
- Fukui, A. 2003. Relationship between seed retention time in bird's gut and fruit characteristics. *Ornitholog. Sci.* **2**(1): 41–48. doi:10.2326/osj.2.41.
- Godschalk, S.K.B. 1985. Feeding behaviour of avian dispersers of mistletoe fruit in the Loskop Dam Nature Reserve, South Africa. *S. Afr. J. Zool.* **20**: 136–146.
- Heer, K., Albrecht, L., and Kalko, E.K.V. 2010. Effects of ingestion by neotropical bats on germination parameters of native free-standing and strangler figs (*Ficus* sp., Moraceae). *Oecologia (Berl.)*, **163**(2): 425–435. doi:10.1007/s00442-010-1600-x. PMID: 20354732.
- Hilhorst, H.W.M. 2007. Definitions and hypotheses of seed dormancy. In *Seed development, dormancy and germination. Edited by B. Kent and H. Nonogaki.* Blackwell, Oxford, U.K. pp. 50–71.
- Holbrook, K.M., and Smith, T.B. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia (Berl.)*, **125**(2): 249–257. doi:10.1007/s004420000445.
- Howe, H.F., and Miriti, M.N. 2004. When seed dispersal matters. *Bioscience*, **54**(7): 651–660. doi:10.1641/0006-3568(2004)054[0651:WSDM]2.0.CO;2.
- Howe, H.F., and Westley, L.C. 1988. *Ecological relationships of plants and animals.* Oxford University Press, Oxford, U.K.
- Hyatt, L.A., Rosenberg, M.S., Howard, T.G., Bole, G., Fang, W., Anastasia, J., Brown, K., Grella, R., Hinman, K., Kurdziel, J.P., and Gurevitch, J. 2003. The distance dependence prediction of the Janzen–Connell hypothesis: a meta-analysis. *Oikos*, **103**(3): 590–602. doi:10.1034/j.1600-0706.2003.12235.x.
- Izhaki, I., Korine, C., and Arad, Z. 1995. The effect of bat (*Rousettus aegyptiacus*) dispersal on seed germination in eastern Mediterranean habitats. *Oecologia (Berl.)*, **101**(3): 335–342. doi:10.1007/BF00328820.
- Lambert, F.R. 1989a. Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. *Ibis*, **131**(4): 521–527. doi:10.1111/j.1474-919X.1989.tb04788.x.
- Lambert, F.R. 1989b. Daily ranging behaviour of three tropical forest frugivores. *Forktail*, **4**: 107–116.
- Levey, D.J., and Duke, G.E. 1992. How do frugivores process fruit? Gastrointestinal transit and glucose absorption in Cedar Waxwings (*Bombycilla cedrorum*). *Auk*, **109**: 722–730.
- Levey, D.J., and Grajal, A. 1991. Evolutionary implications of fruit-processing limitations in Cedar Waxwings. *Am. Nat.* **138**(1): 171–189. doi:10.1086/285210.
- Levey, D.J., Silva, W.R., and Galetti, M. (Editors). 2002. *Seed dispersal and frugivory: ecology, evolution, and conservation.* CABI Publications, Oxford, U.K.
- Linnebjerg, J.F., Hansen, D.M., and Olesen, J.M. 2009. Gut passage effect of the introduced red whiskered bulbul (*Pycnonotus jocosus*) on germination of invasion plant species in Mauritius. *Austral Ecol.* **34**(3): 272–277. doi:10.1111/j.1442-9993.2008.01928.x.
- Lisci, M., and Pacini, E. 1994. Germination ecology of drupelets of the fig (*Ficus carica* L.). *Bot. J. Linn. Soc.* **114**(2): 133–146. doi:10.1111/j.1095-8339.1994.tb01927.x.
- Mayer, A.M., and Poljakoff-Mayber, A. 1989. *The germination of seeds.* 4th ed. Pergamon, Oxford, U.K.
- Murphy, S.R., Reid, N., Yan, Z., and Venables, W.N. 1993. Differential passage time of mistletoe fruits through the gut of honeyeaters and flowerpeckers: effects on seedling establishment. *Oecologia (Berl.)*, **93**(2): 171–176. doi:10.1007/BF00317667.
- Murray, K.G., Russell, S., Picone, C.M., Winnett-Murray, K., Sherwood, W., and Kuhlmann, M.L. 1994. Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. *Ecology*, **75**(4): 989–994. doi:10.2307/1939422.
- Nikolaeva, M.G. 1977. Factors controlling the seed dormancy pattern. In *The physiology and biochemistry of seed dormancy and germination. Edited by A.A. Khan.* Elsevier, Amsterdam, the Netherlands. pp. 51–74.
- Otani, T., and Shibata, E. 2000. Seed dispersal and predation by Yakushima macaques, *Macaca fuscata yakui*, in a warm temperate forest of Yakushima Island, southern Japan. *Ecol. Res.* **15**(2): 133–144. doi:10.1046/j.1440-1703.2000.00330.x.
- Paulsen, T.R., and Högstedt, G. 2002. Passage through bird guts increases germination rate and seedling growth in *Sorbus aucuparia*. *Funct. Ecol.* **16**(5): 608–616. doi:10.1046/j.1365-2435.2002.00668.x.
- Primack, R., and Corlett, R. 2005. *Tropical rain forests: an ecological and biogeographical comparison.* Blackwell, Malden, Mass.
- Ranal, M.A., and Santana, D.G. 2006. How and why to measure the germination process? *Revista Brasileira de Botânica*, **29**(1): 1–11. doi:10.1590/S0100-84042006000100002.
- Renton, K. 2001. Lilac-crowned Parrot diet and food resource availability: resource tracking by a parrot seed predator. *Condor*, **103**(1): 62–69. doi:10.1650/0010-5422(2001)103[0062:LCPDAF]2.0.CO;2.
- Robertson, A.W., Trass, T., Ladley, J.J., and Kelly, D. 2006. Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Funct. Ecol.* **20**(1): 58–66. doi:10.1111/j.1365-2435.2005.01057.x.
- Samuels, A., and Levey, D. 2005. Effects of gut passage on seed germination: do experiments answer the questions they ask? *Funct. Ecol.* **19**(2): 365–368. doi:10.1111/j.1365-2435.2005.00973.x.
- Schupp, E.W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. In *Frugivory and seed dispersal: ecological and evolutionary aspects. Edited by T.H. Fleming and A. Estrada.* Kluwer Academic, Dordrecht, the Netherlands. pp. 15–29.
- Schupp, E.W., Jordano, P., and Gómez, J.M. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytol.* **188**(2): 333–353. doi:10.1111/j.1469-8137.2010.03402.x. PMID: 20673283.
- Shanahan, M., So, S., Compton, S.G., and Corlett, R. 2001. Fig-eating by vertebrate frugivores: a global review. *Biol. Rev. Camb. Philos. Soc.* **76**(4): 529–572. doi:10.1017/S1464793101005760. PMID:11762492.
- Sherwin, C.M. 2006. Guidelines for the treatment of animals in behavioural research and teaching. *Anim. Behav.* **71**(1): 245–253. doi:10.1016/j.anbehav.2005.10.001.
- Short, L.L., and Horne, J.F. 2001. *Toucans, barbets and honeyguides: Ramphastidae, Capitonidae and Indicatoridae.* Oxford University Press, Oxford, U.K.
- Snow, D.W. 1981. Tropical frugivorous birds and their food plants: a world survey. *Biotropica*, **13**(1): 1–14. doi:10.2307/2387865.
- Sorensen, A.E. 1984. Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). *J. Anim. Ecol.* **53**(2): 545–557. doi:10.2307/4533.
- StatSoft Inc. 2001. *STATISTICA.* Version 6. Statsoft Inc., Tulsa, Okla.
- Tewksbury, J.J., Levey, D.J., Huizinga, M., Haak, D.C., and Traveset, A. 2008. Costs and benefits of capsaicin-mediated control of gut retention in dispersers of wild chilies. *Ecology*, **89**(1): 107–117. doi:10.1890/07-0445.1. PMID:18376552.
- Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspect. Plant Ecol. Evol. Syst.* **1**(2): 151–190. doi:10.1078/1433-8319-00057.

- Traveset, A., and Verdú, M. 2002. A meta-analysis of the effect of gut treatment on seed germination. *In* Seed dispersal and frugivory: ecology, evolution and conservation. *Edited by* D.J. Levey, W.R. Silva, and M. Galetti. CAB International, Wallingford, U.K. pp. 339–350.
- Traveset, A., Riera, N., and Mas, R.E. 2001. Passage through bird guts cause interspecific differences in seed germination characteristics. *Funct. Ecol.* **15**(5): 669–675. doi:10.1046/j.0269-8463.2001.00561.x.
- Traveset, A., Robertson, A.W., and Rodríguez-Pérez, J. 2007. A review on the role of endozoochory in seed germination. *In* Seed dispersal theory and its application in a changing world. *Edited by* A.J. Dennis, W.W. Schupp, R.J. Green, and D.A. Westcott. CAB International, Wallingford, U.K. pp. 78–103.
- Traveset, A., Rodríguez-Pérez, J., and Pías, B. 2008. Seed trait changes in dispersers' guts and consequences for germination and seedling growth. *Ecology*, **89**(1): 95–106. doi:10.1890/07-0094.1. PMID:18376551.
- Westcott, D.A., Bentrupperbäumer, J., Bradford, M.G., and McKeown, A. 2005. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia (Berl.)*, **146**(1): 57–67. doi:10.1007/s00442-005-0178-1.
- Wotton, D.M., Clout, M.N., and Kelly, D. 2008. Seed retention times in the New Zealand pigeon (*Hemiphaga novaeseelandiae*). *N.Z. J. Ecol.* **32**: 1–6.
- Yagihashi, T., Hayashida, M., and Miyamoto, T. 1998. Effects of bird ingestion on seed germination of *Sorbus commixta*. *Oecologia (Berl.)*, **114**(2): 209–212. doi:10.1007/s004420050438.
- Yahya, H.A.S. 2001. Biology of Indian barbets. Authors Press, New Delhi, India.
- Zar, J.H. 1999. Biostatistical analysis. Prentice Hall, Inc., Upper Saddle River, N.J.