

Songbird dispersal of American ginseng (*Panax quinquefolius*)

Author(s): Amy M. HRUSKA, Sara SOUTHER and James B. MCGRAW

Source: *Écoscience*, 2014, Vol. 21, No. 1, Special issue (1st part, pages 1–33) / Numéro thématique (1re partie, pages 1–33) (2014), pp. 46–55

Published by: Taylor & Francis, Ltd.

Stable URL: <https://www.jstor.org/stable/10.2307/26613648>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



Taylor & Francis, Ltd. is collaborating with JSTOR to digitize, preserve and extend access to *Écoscience*

JSTOR

Songbird dispersal of American ginseng (*Panax quinquefolius*)¹

Amy M. HRUSKA², Department of Biology, West Virginia University, Morgantown,
West Virginia 26506, USA, e-mail: hruska.amy@gmail.com

Sara SOUTHER, Department of Biology, University of Wisconsin-Madison,
Madison, Wisconsin 53706, USA.

James B. MCGRAW, Department of Biology, West Virginia University,
Morgantown, West Virginia 26506, USA.

Abstract: American ginseng (*Panax quinquefolius*) is an uncommon perennial understory herb found in eastern deciduous forest. The species is harvested for the international medicinal plant trade. While previous research has inferred that seed dispersal is limited, the production of bright red, fleshy berries suggests long-distance dispersal may be facilitated by songbirds. The objective of this study was to determine how songbirds interacted with ginseng and whether they dispersed or predated ginseng seeds. We used infrared, motion-activated cameras to observe animal–ginseng interactions in the field. To determine the disperser potential of songbirds observed visiting ginseng in the field, we conducted a captive feeding study at the Tennessee Aquarium. Thrushes removed berries from ginseng infructescences more frequently, compared to other potential dispersers, and regurgitated viable seeds 5–37 minutes after ingestion in feeding trials. By dispersing ginseng seeds, thrushes provide a mechanism for ginseng to improve its probability of persistence in the face of 3 primary threats to populations: deer browse, harvest, and climate change.

Keywords: American ginseng, songbird dispersal, wood thrush.

Résumé: Le ginseng à 5 folioles (*Panax quinquefolius*) est une herbe vivace peu commune que l'on trouve dans le sous-étage des forêts feuillues de l'Est. L'espèce est récoltée pour le commerce international des plantes médicinales. De précédentes recherches ont suggéré que la dispersion des graines de cette plante est limitée. Cependant, la production de baies charnues rouge vif laisse croire que la dispersion des graines sur de longues distances pourrait être facilitée par les oiseaux chanteurs. L'objectif de cette étude était d'examiner la nature des interactions entre les oiseaux chanteurs et le ginseng et de déterminer si les oiseaux représentent des agents de dispersion ou des prédateurs pour les graines du ginseng. Nous avons utilisé des caméras infrarouges activées par le mouvement pour observer les interactions oiseau-ginseng sur le terrain. Afin de connaître le potentiel des oiseaux chanteurs comme agent de dispersion du ginseng, nous avons réalisé des essais d'alimentation avec des oiseaux en captivité à l'aquarium du Tennessee. Ce sont les grives qui récoltaient le plus souvent les baies d'infructescences du ginseng, comparées à d'autres agents potentiels de dispersion, et elles régurgitaient des graines viables de 5 à 37 minutes après l'ingestion dans les essais d'alimentation. En dispersant les graines du ginseng, les grives fournissent un mécanisme permettant à cette plante d'améliorer sa probabilité de persistance face à 3 menaces principales pour ses populations : le broutement par le cerf, la récolte et les changements climatiques.

Mots-clés: dispersion par des oiseaux chanteurs, ginseng à 5 folioles, grive des bois.

Nomenclature: Kartez, 1994; Wilson & Reeder, 2005; American Ornithologists' Union, 2012.

Introduction

American ginseng (*Panax quinquefolius*) is a forest herb found throughout much of eastern North America's deciduous forests. The species is well known for its medicinal properties (Johannsen, 2006). Annually, hundreds of thousands of wild ginseng roots are harvested and sold into the international medicinal plant trade (Division of Management Authority, 2012), generating millions of dollars in supplemental income for harvesters (Robbins, 2000). Concerns about overharvest of ginseng led to its listing on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)

in 1975 and resulted in monitoring of the international export of American ginseng roots (Robbins, 2000).

In addition, American ginseng is a long-lived, perennial herb found in thousands of small populations throughout Appalachian forests that are characterized by a clustered spatial distribution of individuals within populations (McGraw, Sanders & Van der Voort, 2003; Cruse-Sanders & Hamrick, 2004a). Due to its economic importance, a life cycle similar to many other understory herbs, and its wide spatial distribution comprised of thousands small populations, American ginseng has become a model species for investigating a plethora of demographic and conservation-based questions. Extensive research has been conducted investigating the demography of American ginseng and how various environmental factors influence individual plant performance (reviewed in McGraw *et al.*, 2013). These research studies have found that in addition to the

¹ Rec. 2014-02-19; acc. 2014-06-02.

Associate Editor: Daniel Gagnon.

² Author for correspondence.

DOI 10.2980/21-1-3679

negative impacts of ginseng harvest, deer herbivory and climate change are 2 environmental factors also negatively impacting the population growth of ginseng (reviewed in McGraw *et al.*, 2013). However, a critical aspect of ginseng demography that remains poorly understood is its dispersal (Cruse-Sanders & Hamrick, 2004a,b; McGraw *et al.*, 2013).

Dispersal influences the spatial distribution, gene flow, and evolution of a species. Seed dispersal increases the distance between parent and offspring, thereby reducing competition and disease transmission between the parent and offspring, and among siblings, as well as decreasing other intraspecific interactions between individuals within a population (Augsburger, 1984). Dispersal reduces inbreeding with relatives, but in species such as ginseng that display Allee effects (Hackney & McGraw, 2001), it may isolate individuals from potential mates, increasing the degree of selfing. Seed dispersal also facilitates the expansion of a population as well as the establishment of new populations (Howe & Smallwood, 1982; Clark & Clark, 1984; Clark *et al.*, 2007). Recent concerns over the potential for populations and species to shift distribution in response to changing climate have highlighted the need for a comprehensive investigation of plant dispersal mechanisms (*e.g.*, Pearson & Dawson, 2003; Thuiller *et al.*, 2008; Engler & Guisan, 2009). American ginseng is a species adapted to local temperature conditions, and determining its dispersal mechanisms is important for understanding both the current and future distributions of populations (Souther & McGraw, 2011). Dispersal away from deer trails or to new sites away from populations known by human harvesters could also be important to persistence of ginseng.

To date, American ginseng seeds have been considered to be gravity dispersed (Lewis & Zenger, 1982; Van der Voort, 2005). Gravity dispersal results in short-distance dispersal events for plant species and is often combined with one or more other dispersal mechanisms (Vittoz & Engler, 2007). American ginseng produces fleshy, red berries, suggesting animal-facilitated seed dispersal (Howe & Smallwood, 1982; McGraw *et al.*, 2013). The best-documented ginseng–animal interaction is by white-tailed deer (*Odocoileus virginianus*). However, feeding trials showed that seeds were rendered inviable when berries were ingested (Furedi & McGraw, 2004). Other ginseng seed–animal interactions have only been the subject of anecdotes, though phenology and morphological characteristics of ginseng berries suggest songbirds may facilitate ginseng dispersal (Pritts, 2010).

Green ginseng berries begin to form in mid-July and ripen to red throughout August and September (McGraw *et al.*, 2005). While some songbirds are frugivorous year-round, many migratory songbirds switch from an insectivorous diet to a frugivorous diet during the fall prior to migration, resulting in an increased demand for fruits (Stiles, 1980; Izhaki & Safriel, 1989). Additionally, songbirds are particularly attracted to fruits that have a strong contrast against foliage, resulting in a diet of fruits that are primarily purple, red, or black in colour (Schmidt & Schaefer, 2004; Iluz, 2011). Ginseng berries contain 1–3 seeds and when ripe can range from 5 to 15 mm in size, with seeds that are less than 5 mm. The ability of

frugivorous bird species to ingest fruit has been shown to be limited by the width of the gape, particularly for species that gulp, or ingest, the whole fruit (Wheelwright, 1985; Piper, 1986; Jordano, 1987; Levey, 1987; Lambert, 1989). The small size of American ginseng seeds would theoretically allow them to be ingested by a majority of songbird species within its range (Meyer & Witmer, 1998). Furthermore, ginseng seeds have a hard exterior coat that may prevent damage to the embryo after ingestion and possibly enable it to pass through a bird's gizzard (Cousens, Dytham & Law, 2008).

The overall objective of this study was to investigate songbirds as potential seed dispersers of American ginseng. Specifically, we asked: 1) What is the frequency and “intimacy” of animal–ginseng interactions, particularly songbird interactions? 2) What proportion of berries is removed as the result of ginseng–animal interactions? 3) Is there a difference in the frequency and “intimacy” of avian–ginseng interactions compared to mammalian–ginseng interactions? 4) Of the avian interactions, what songbird species most frequently interact with ginseng? 5) Do songbirds that interact with ginseng defecate or regurgitate viable seeds? 6) How long do ginseng seeds stay within a songbird's digestive system? The answers to these questions provide critical information regarding how ginseng is dispersed across the landscape and ultimately can be used to create more accurate demographic models of ginseng.

Methods

FIELD INVESTIGATION OF SONGBIRD–GINSENG INTERACTIONS

To determine whether songbirds interact with American ginseng and how close their interactions are, Moultrie D40 (Birmingham, AL, USA) infrared, motion-activated wildlife cameras were placed within 6 wild ginseng populations near Morgantown, West Virginia from 2007 to 2013 (total populations/year: 1/2007; 3/2009; 2/2010; 2/2011; 3/2012; 2/2013). One to 3 cameras were set up per site in mid-August, once berries began to ripen from green to red. Most often, cameras were removed once berries were absent from the infructescence or the plant had senesced. Wildlife cameras were positioned on 1.3-m tall, 5- × 10-cm camouflage-painted wooden stakes, at a distance of 1–2 m from a focal reproductive plant or cluster of reproductive plants within a population. Cameras could be triggered and record images at any time, day or night. For each instance that a camera was triggered by an infrared movement, the wildlife cameras were set to take 3 images. These 3 images were used to define a single potential dispersal event. The cameras were also programmed to have a 1-min delay between each of these events.

Potential dispersers were identified within each event, and a value was assigned to the event that corresponded to the level of interaction a potential disperser had with the focal ginseng plant(s). Events were categorized based on a 0–5 scale, where 0 represented the lowest level of interaction, no apparent potential disperser within the image (but something triggered the camera), and 5 represented the highest level, with berries clearly removed by the potential disperser from the ginseng infructescence (Table I).

TABLE I. Each interaction event, made up of a series of 3 images per infrared motion-activated occurrence, was assigned a quantitative value to represent the level of interaction a potential disperser (PD) had with American ginseng berries.

Level of interaction	Value	Description
None	0	No PD is located within the photograph.
Low	1	The PD is in photograph and not under the canopy ^a of the ginseng plant for 2 or more images.
	2	The PD is under the canopy ^a of the ginseng plant for either 2 or 3 images, but it is not foraging ^b .
	3	The PD is under the canopy of the plant in question for either 2 or 3 images and is foraging ^b .
High	4	The PD has touched the infructescence.
	5	A berry goes missing between 2 events, with at least 1 of the events having an identifiable PD.
		There is a berry in the PD's possession.
		Within the three-image sequence of an event, a berry has been removed from the infructescence.

^a Under canopy: the potential disperser appears below the leaves of the focal ginseng plant.

^b Foraging: the potential disperser has its nose or beak to the ground below the leaves of the focal ginseng plant.

Only images where a portion of or all berries had ripened were used for calculations and analyses. Summary statistics included 1) mean number of events per camera-day, 2) frequency of potential dispersers within a given level of interaction, 3) proportion of events with no visible potential disperser, 4) proportion of berries missing per plant after a level 4 or 5 interaction with a potential disperser, 5) total proportion of overall potential dispersers that were avian or mammalian, and 6) proportion of potential dispersers that were avian and mammalian per level of interaction. For those events containing a potential disperser, a log-likelihood analysis was performed using SAS JMP Statistical Software v11.0 (SAS Institute, Cary, North Carolina, USA) to determine whether avian potential dispersers more frequently had high-level interactions with ginseng compared to mammalian potential dispersers. Additionally, given the types of avian potential dispersers observed within the images, a second log-likelihood analysis compared the level of interaction that thrush species (family: Turdidae) and non-thrush avian potential dispersers had with ginseng. Thrush species that could have been observed in the field included American robin (*Turdus migratorius*), gray-cheek thrush (*Catharus minimus*), hermit thrush (*Catharus guttatus*), Swainson's thrush (*Catharus ustulatus*), wood thrush (*Hylocichla mustelina*), and veery (*Catharus fuscescens*).

INVESTIGATION OF THRUSHES AS POTENTIAL DISPERSERS

Based on the field observation of thrushes as one of the most frequent potential avian dispersers, feeding trials were conducted with 4 captive thrushes at the Tennessee Aquarium from September 5 to 8, 2013. Over the course of 2.5 d, ginseng berries were fed *ad libitum* to a hermit thrush, a Swainson's thrush, a veery, and a wood thrush. Due to renovations to their normal exhibit, the hermit thrush, Swainson's thrush, and veery were maintained in a cage environment (47.5 × 47.5 × 90 cm) and had been living there for 4 weeks. While the hermit thrush was placed in a cage by itself, the Swainson's thrush and veery were caged together due to space limitations. Additionally, due to space limitations, the wood thrush could not also be caged, and feeding trials for this species were conducted within the "Delta Country Exhibit" (ca 1200 m²), which included vegetation as well as other bird species.

Berry production is low in natural populations, so ginseng berries for feeding trials were obtained from a ginseng cultivator using "woods grown" growth methods (under natural tree canopy). Berries were collected directly from plants 2 d prior to the feeding trials and were stored at 4 °C. Ginseng berries were offered detached from infructescences within feeding trays, during the normal feeding time (08:00 to 17:00). During the first day and for the morning of the second day, berries were offered simultaneously with normal food items (mealworms, sunflower seeds, etc.) in order to minimize stress to the birds in case they rejected the fruit. Berries were offered as the sole food item for the remaining trials during the afternoon of the second day and the morning of the third day, after birds had been observed ingesting the berries.

Within the exhibit that held the wood thrush, at least 2 observers were present to record wood thrush feeding behaviour, given that the bird still had free movement within the exhibit and other species that could potentially eat the berries were present. Video cameras were used to record the behaviour of the caged birds. Primary observations were made regarding the digestive behaviours (whether seeds were defecated or regurgitated) of the thrushes and the amount of time between ingestion and an exhibited digestive behaviour. Additional observations were made regarding the total number of berries that were eaten by each bird, the proportion of one-seeded and two-seeded berries eaten, and, in the wood thrush exhibit, the number of other avian species that interacted with and the type of interactions they had with the ginseng berries. Recovered seeds that had been ingested were tested for embryo viability using a 0.1% tetrazolium chloride solution (Baskin & Baskin, 2001).

Results

FIELD INVESTIGATION OF SONGBIRD–GINSENG INTERACTIONS

In total, 15 wildlife cameras were used from 2007 to 2013, resulting in 241 camera-days and a total of 925 camera-triggered events (2775 total images). Wildlife cameras were triggered 3.9 ± 0.3 (mean \pm SE) times per camera-day, with a range of 0–35 triggered events per camera-day. Of the original cameras deployed, image collection for 3 cameras (1:2009; 1:2010; 1:2013) ended prematurely due to

battery drain or a camera malfunction and therefore images of potential dispersers were not collected after berries had ripened. Additionally, a total of 8 camera trials were not able to be included in analyses because memory cards were stolen (4:2009; 3: 2012; 1; 2013), likely because of the illegal harvest of the focal plant(s). Of the total 925 triggered events, 647 events had no potential disperser (Level 0 interaction; Table I), 230 had mammalian potential dispersers, and 48 had avian potential dispersers.

A majority (83.1%) of the events for both avian and mammalian potential dispersers were categorized as a Level 1 interaction. Of the interaction levels that involved direct interaction with a ginseng infructescence and berries (Levels 4 and 5), mammals were categorized most frequently as Level 4 interaction, while avian dispersers were categorized most frequently as Level 5 interactions (Table II). On average, 2 berries were missing from an infructescence following a Level 4 or 5 interaction by a potential disperser for every 7 berries available (± 0.085). The maximum number of berries missing from focal infructescences as the result of or following Level 4 and 5 avian interactions was 6 (Table III), whereas 1 was the maximum number missing or removed from focal infructescences following Level 4 and 5 mammalian interactions (Table III).

In order to have enough replication to statistically compare mammalian and avian dispersers, the levels of interaction were simplified. Levels 1–3 were combined into a single category we term “Low Level” because these included behaviours that did not involve direct interaction with the ginseng infructescence and were therefore least likely to result in a dispersal event. Levels 4 and 5 were combined into a category we refer to as “High Level”

because they included behaviours involving direct interaction with the ginseng infructescence and were most likely to result in a dispersal event. Mammalian and avian dispersers were significantly different in the proportion of Low and High Level interactions with ginseng berries (Figure 1; likelihood ratio $\chi^2 = 19.88, p < 0.0001$). While mammalian potential dispersers most frequently triggered the wildlife cameras, avian potential dispersers were captured most frequently interacting directly with ginseng berries (Figure 1).

Squirrel species (family: Sciuridae), accounted for 60.8% of the 230 mammalian potential dispersal events. Eastern chipmunks (*Tamias striatus*) were the most frequent potential dispersers ($n = 104$), followed by mice (*Peromyscus* sp., family: Cricetidae) ($n = 36$) and Eastern gray squirrels (*Sciurus carolinensis*) ($n = 35$). Of the mammalian potential dispersers, only chipmunks interacted with ginseng berries at the High Level of interaction (Figure 2), but foraging behaviour below focal ginseng plants (Level 3 interaction) was observed among chipmunks and squirrels (Table II).

Of the avian potential dispersers, thrush species accounted for 81.3% of the 48 avian events. The most common avian potential dispersers were wood thrushes ($n = 27$), followed by American robins (*Turdus migratorius*) ($n = 6$) and hermit thrushes ($n = 5$) (Table II). Using the Low and High levels of interaction, thrush species were found to differentially interact with ginseng relative to other avian potential dispersers (likelihood ratio $\chi^2 = 4.140; p = 0.0419$), and were found to most frequently interact with the infructescence and berries (Figure 3). The 3 thrush species that were found to interact with the infructescence and ginseng berries were wood thrushes ($n = 7$), hermit thrushes ($n = 2$), and a Swainson’s thrush ($n = 1$) (Figure 3).

TABLE II. The total number of events for each mammalian and avian species per levels of interaction.

Disperser type	Level of interaction				
	Low		High		
	1	2	3	4	5
Mammalian	197	18	10	4	1
Eastern chipmunk	83	Eastern chipmunk 10	Eastern chipmunk 7	Eastern chipmunk 4	Eastern chipmunk 1
Mouse (multiple sp.)	33	Eastern gray squirrel 4	Eastern gray squirrel 2		
Eastern gray squirrel	29	Mouse (multiple sp.) 3	Fox squirrel 1		
Raccoon	21	Virginia opossum 1			
Virginia opossum	17				
White-tailed deer	6				
Fox squirrel	3				
Fisher	2				
Weasel	2				
Cotton-tail rabbit	1				
Avian	35	3	0	1	9
Wood thrush	18	Wood thrush 2	N/A	Wood thrush 1	Wood thrush 6
American robin	6	Crow 1			Hermit thrush 2
Ovenbird	3				Swainson's thrush 1
Hermit thrush	3				
Unidentified thrush	1				
Turkey	1				
Eastern towhee	1				
Tufted titmouse	1				
Cardinal	1				
Total	232	21	10	5	10

TABLE III. The total number of berries removed per camera location following a Level 4 or 5 interaction with a potential disperser, and the species responsible for the berry removal at each camera location, where n is the number of berries missing due to an animal interaction.

Camera ID	Berries removed	Berry total	Interacting species
FCF1	6	6	Wood thrush ($n = 6$)
TPW1	4	8	Wood thrush ($n = 3$) Hermit thrush ($n = 1$)
TPG	2	3	Swainson's thrush ($n = 1$) Eastern chipmunk ($n = 1$)
FCF3	2	4	Wood thrush ($n = 2$)
FCF2	1	3	Hermit thrush ($n = 1$)
AF2	1	3	Eastern chipmunk ($n = 1$)
AF1	1	2	Eastern chipmunk ($n = 1$)
WL2	1	8	Eastern chipmunk ($n = 1$)
P41	0	3	N/A
TP1	0	10	N/A
TPR2	0	4	N/A
TPW2	0	5	N/A
TPRC	0	2	N/A
WL1	0	3	N/A
TPR1	N/A	N/A	N/A

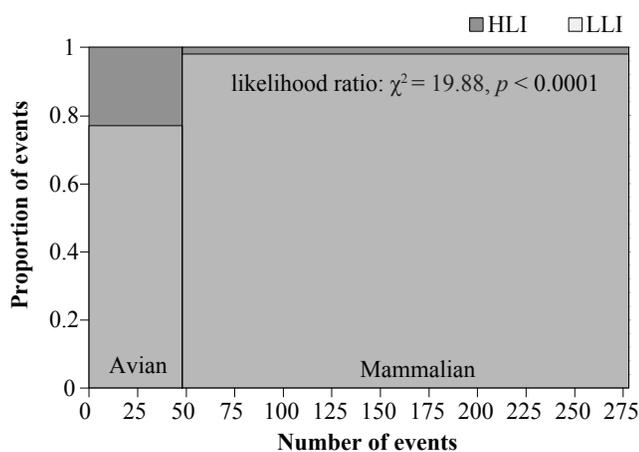


FIGURE 1. Partitioning of avian and mammalian potential disperser events based on categories that would least likely result in a dispersal event (LLI: Low Level of Interaction) and most likely result in a dispersal event (HLI: High Level of Interaction).

INVESTIGATION OF THRUSHES AS POTENTIAL DISPERSERS

Over the course of two and a half days, a total of 80 berries were offered within the wood thrush exhibit, 80 berries within the hermit thrush cage, and 61 berries to the veery and Swainson's thrush. All thrushes ingested at least 1 berry, with the wood thrush ingesting the highest number of berries over the course of two and a half days. Ingested seeds were regurgitated by all thrushes, with an average time of 15 min 55 s \pm 3 min 44 s ($n = 9$) between ingestion and regurgitation. The wood thrush ingested a total of 12 berries. Seven wood thrush regurgitation events were observed, with 5 events occurring after a specific and isolated feeding event. Of these isolated regurgitation events, a mean time of 2 min 12 s \pm 3 min 35 s, with a minimum time of 15 min and a maximum of 37 min, between ingestion and regurgitation was observed.

The veery ingested only 2 berries, both one-seeded, and had a mean time of 7 min 15 s \pm 2 min 43 s between ingestion and regurgitation. The Swainson's thrush ingested a single, two-seeded berry during the study and regurgitated the first seed 5 min 33 s after ingestion and the second seed 7 min 14 s after ingestion. The hermit thrush did eat 1 berry over the course of the study, but the time until regurgitation was not recorded. However, given that the seed of the missing berry was recovered, clean of pulp and without feces, it was determined that a regurgitation event had occurred. A total of 8 seeds that had been regurgitated were recovered (wood thrush: 3; Swainson's and veery: 4; hermit thrush: 1). All recovered seeds were found to be viable by the tetrazolium test after regurgitation.

Other bird species within the Delta exhibit at the Tennessee Aquarium ingested ginseng berries. Of the 80 berries offered within the exhibit, cardinals (*Cardinalis cardinalis*) ate 47 berries, a summer tanager (*Piranga rubra*) ate 4 berries, and a cedar waxwing (*Bombycilla cedrorum*), a brown thrasher (*Toxostoma rufum*), and an orchard oriole (*Icterus spurius*) each ate 1 berry. While most of the other species that ate berries were not observed for their digestive behaviours, the cardinals predated the ginseng seed by removing the pulp and seed coat from the ginseng seed and ingesting the unprotected interior of the seed containing the plant embryo.

Discussion

Before interpreting camera-trap results, it is important to address possible bias due to the technology itself. Previous work with infrared, motion-activated wildlife cameras has shown that there is uncertainty as to what triggers an event not only between different models of cameras, but also between individual cameras of the same model (Swann *et al.*, 2004; Hughson, Darby & Dungan, 2010). While we tried to decrease this uncertainty by mounting cameras in a systematic fashion, a number of events that triggered the cameras during this study did not result in a visible potential disperser within the images. Three explanations for these uninformative images are possible: 1) the camera is triggered by something other than an animal, 2) the camera is triggered by a potential disperser that is out of frame or is hidden at the time of shutter release and therefore is not in the image (Swann *et al.*, 2004), or 3) the camera is triggered by a potential disperser, but very effective camouflage results in the observer falsely concluding that no animal is present. False triggers may occur due to environmental factors, such as the wind moving either vegetation or the camera mount (Swann *et al.*, 2004). This cause would not bias the potential disperser information obtained by the camera, but the other 2 causes could bias the set of images obtained in favour of slower moving, larger, or more visible animals. By setting the cameras to take 3 images per event, these errors can be reduced in frequency at the analysis stage by carefully toggling between the images to detect movement within the event.

While an unknown bias in the frequency of capture of different species may have occurred, these cameras nevertheless provide a simple and sophisticated methodology



FIGURE 2. a) Image of an Eastern chipmunk demonstrating High Level interaction behaviour by touching the ginseng infructescence. b) Image of a wood thrush demonstrating High Level interaction behaviour with a berry in its beak. c) Image of a hermit thrush demonstrating High Level interaction behaviour with a berry in its beak. d) Image of a Swainson's thrush demonstrating High Level interaction behaviour with a berry in its beak.

for observing plant–animal interactions that would be impossible by direct observation. By using wildlife cameras, a total of 5784 h (241 camera-days) of observation time were logged, resulting in sequences of images that were then analyzed carefully in a lab setting. Additionally, wildlife cameras are less intrusive than human observers, which can stress wildlife and decrease the probability of an animal–ginseng interaction (Cutler & Swann, 1999).

Using wildlife cameras to observe animal interactions with American ginseng, we have determined that animal–ginseng interactions are variable in intensity and not as rare as previously thought. Five percent of all events with potential dispersers were categorized as High Level interactions. While these did not occur at every camera location, they resulted in removal of all of the berries from an infructescence at 1 of the camera locations (Table III). Of the potential dispersers observed, thrushes, particularly wood thrushes, most frequently removed berries directly from the plants, but chipmunks also had High Level interactions with ginseng infructescences. Additionally, interactions categorized as Level 3 in the Low Level interactions demonstrate foraging below the ginseng plants; these events may have resulted in secondary dispersal by small mammals (Vander Wall, Kuhn, & Gworek, 2005; Vander Wall & Beck, 2012). Many perennial understory herbs such as

ginseng do not produce large crops or large seeds, which may make them a low preference item for small mammals, increasing the seeds' probability of survival after being cached (Barga & Vander Wall, 2013). However, small mammal–seed interactions can be highly variable and, in the case of small seeds, can result in seed predation events, which could contribute to ginseng population decline (*e.g.*, Fenner, 2000; Vander Wall, 2010; Rusch, Midgley & Anderson, 2013). High Level thrush–ginseng interactions are most frequently represented in the data, making thrushes the most likely candidate for animal dispersal events beyond the distances recorded for dispersal by gravity (Van der Voort, 2005).

Wood thrushes may have been the most common avian species to trigger an event because their breeding habitat range is nearly identical to that of American ginseng (Sibley, 2000). Hermit thrushes and Swainson's thrushes, the other 2 thrush species to have High Level interactions, have a more northern breeding range and may be more likely to interact with ginseng in the northern portion of ginseng's range (Sibley, 2000). Additionally, the veery, a species that was not observed on camera but was fed during the captive feeding trials, may not have been detected during field observations because their breeding range

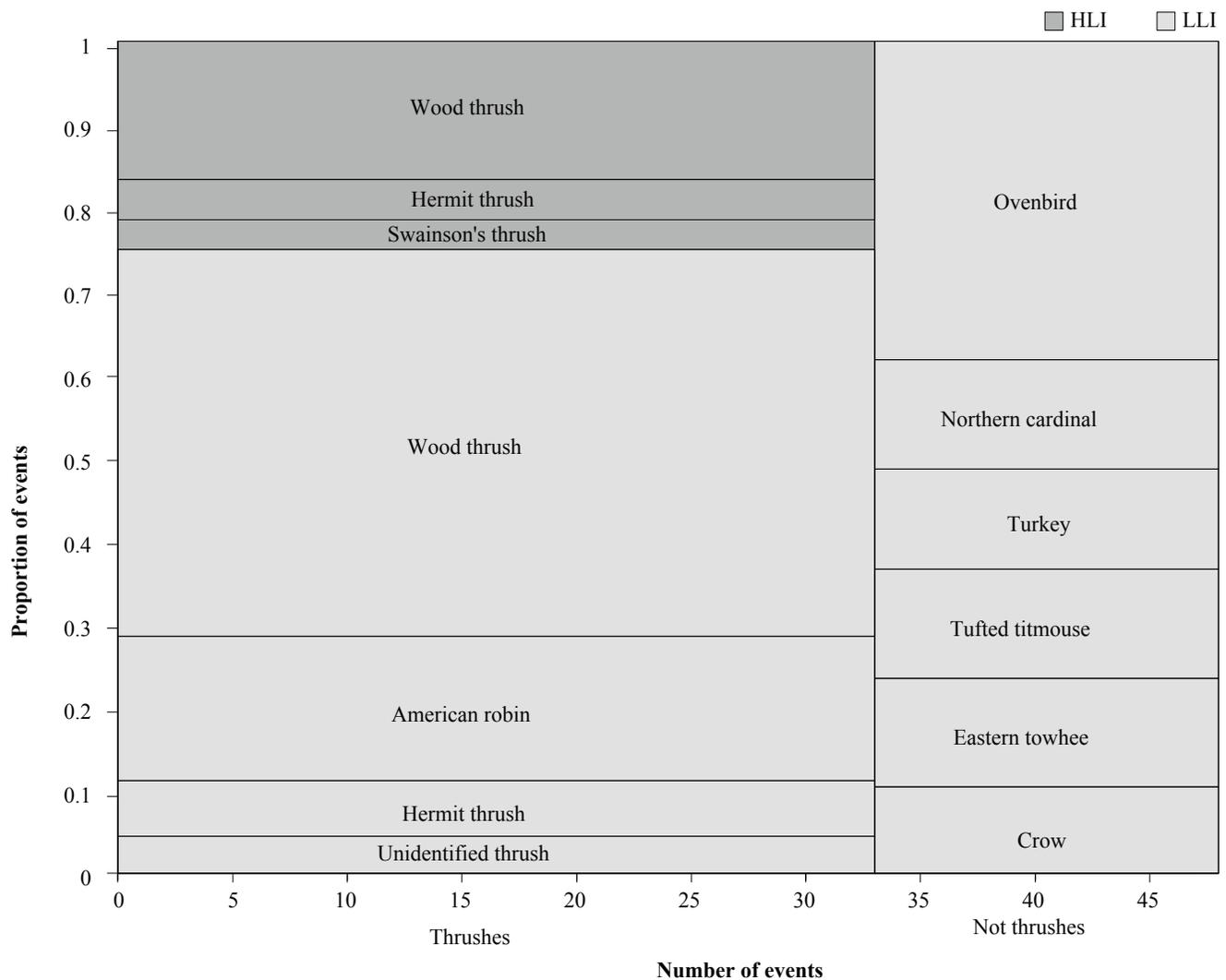


FIGURE 3. Partitioning of thrush and non-thrush potential disperser events based on categories that would least likely result in a dispersal event (LLI: Low Level of Interaction) and most likely result in a dispersal event (HLI: High Level of Interaction), with the proportion of species within each category.

barely overlaps the northern portion of the region where wildlife cameras were placed (Sibley, 2000). But they too could ingest ginseng pre-migration and at stopover sites en route to their wintering grounds.

Our feeding studies demonstrated that after berries were ingested by a thrush species, viable ginseng seeds were regurgitated. Meyer and Witmer (1998) demonstrated that the germination of similar seeds with similar germination requirements (spicebush: *Lindera benzoin*; arrowwood viburnum: *Viburnum dentatum*; chokecherry: *Prunus virginiana*) were not affected by thrush regurgitation when grown in a controlled greenhouse setting. Given that ginseng has a high natural germination rate in the field (germination probabilities as high as 80% in the field; reviewed in McGraw *et al.*, 2013), if germination is not hindered by thrush regurgitation, there is a high probability that seeds dispersed by thrushes will germinate and persist when dispersed to a suitable site.

The distances traveled between ingestion and regurgitation sites are expected to be shorter than distances traveled

between ingestion and defecation sites, given the amount of time the seeds stay within a bird's digestive system (*e.g.*, Meyer & Witmer, 1998; Clark *et al.*, 2005; Uriarte *et al.*, 2011). On average, ginseng seeds were regurgitated after 16 min, which is consistent with other recorded thrush regurgitation times for seeds of similar sizes (*L. benzoin*, *V. dentatum*, *P. virginiana*; Meyer & Witmer, 1998).

Contrasting behaviours exhibited by adults and juveniles during the seed dispersal season may result in different sets of dispersal distances for ingested ginseng seeds. Post-breeding adult wood thrushes relocate 550–7000 m from nesting sites to new molting sites (Vega Rivera *et al.*, 1999). While these distances may not be traversed within 1 flight, they do tend to occur during late July and early August and can overlap with the early ripening of ginseng berries (Vega Rivera *et al.*, 1998b; McGraw *et al.*, 2005). However, once adult thrushes begin their pre-migration molt, which is centred on the ginseng seed ripening period, their ability to fly is drastically reduced. This causes them to become secretive and find areas of dense forest cover and

high food abundance in order to avoid predator detection (Vega Rivera *et al.*, 1998b). During their molt, adult thrush mobility decreases by almost 50% compared to movement during breeding season (Vega Rivera *et al.*, 1999), suggesting that adult thrushes will most likely move seeds less than 100 m between ingestion and regurgitation sites during their molt. Smith *et al.* (2004) observed a 70% probability that a hermit thrush will disperse a seed less than 100 m from the ingestion site over a 45-min time period during the winter season, but this distance may underestimate hermit thrush movement during the fall because hermit thrushes are primarily territorial on their wintering grounds (Brown, Strong & Stouffer, 2000).

Juvenile thrushes, however, undergo a pre-basic molt prior to migration and spend time searching for optimal foraging sites and making exploratory movements (Vega Rivera *et al.*, 1998a) when ginseng berries are ripe (McGraw *et al.*, 2005). After leaving the natal site, young thrushes will travel 150 m, on average, to a dispersal site and will travel to as many as 4 different dispersal sites before their migration (Vega Rivera *et al.*, 1998a). Within these dispersal sites, juveniles move approximately 100 m between consecutive locations and occasionally make exploratory movements greater than 300 m from the dispersal site (Vega Rivera *et al.*, 1998a). The larger range of mobility of juvenile thrushes provides an opportunity for rapid seed dispersal beyond 100 m.

Very long distance dispersal (hundreds of kilometers) of ginseng seeds by thrushes undertaking their annual migration will likely be rare, both because retention of seeds is relatively short-lived and because the probability of ingesting a ginseng seed as the last meal prior to taking flight is low. Dispersal during migration is also unlikely to be effective as a mechanism for responding to climate change, since the direction of movement would be opposite to that which would enable populations to track their preferred temperature zones (Souther & McGraw, 2011). Nevertheless, movement of seeds by thrushes on the order of hundreds of meters, particularly movement up in elevation, could be important for tracking climate change.

American ginseng is a species that was once abundant throughout Appalachian forest but is now located in thousands of small populations with a clustered spatial distribution (Cruse-Sanders & Hamrick, 2004a; McGraw *et al.*, 2013). While seed dispersal has been previously considered to be primarily via gravity, and therefore limited, our findings strongly suggest that dispersal events by thrushes are not rare. The variation of High Level thrush–ginseng interactions between camera locations from frequent to absent suggests that variation in habitat suitability for post-breeding thrushes (Ozinga *et al.*, 2004; Russo, Portnoy & Augspurger, 2006) will determine the frequency of such dispersal events.

American ginseng's broad niche may enable it to persist in sites where thrush populations are low or nonexistent. Populations in these sites would likely be confined to smaller areas and would tend to be found in 1 or a few isolated patches rather than many dispersed

clusters (Cruse-Sanders & Hamrick, 2004a). However, ginseng growing in habitats that provide an abundance of food resources and protective cover would be more likely to have frequent interactions with thrushes and a greater probability for dispersal beyond 2 m, as well as for long-distance dispersal events in areas with a higher number of juvenile thrushes. Dispersal across the landscape by thrushes could produce not only many new subpopulations within a population, but also new populations across the landscape. Most demographic models for plants assume random disperser movements, but movement is most often the result of non-random behaviours (Schupp, Jordano & Gómez, 2010). In order to incorporate these data into a spatially explicit demographic model for ginseng, research investigating the specific types of habitats where both thrushes and ginseng are present, their population densities, and their movement patterns on a minute time scale is needed.

With thrushes now known to be primary seed dispersers, the recovery and conservation of thrush and ginseng populations in North America are connected. Thrush populations have been declining in North America since the late 1960s due to habitat loss, fragmentation, and degradation, *e.g.*, acid rain and brown-headed cowbird parasitism (Trine, 1998; Hames *et al.*, 2002; Betts *et al.*, 2010). Ginseng provides a source of food for thrushes prior to migration, and thrush dispersal of ginseng seeds in turn could improve ginseng's resilience in the face of the 3 most important factors shown to be causing population decline: deer browse, harvest, and climate change (McGraw *et al.*, 2013). Thrush dispersal provides the opportunity for ginseng to be dispersed away from areas with heavy deer traffic and areas of intense foraging, which is important because, in addition to having negative effects as herbivores (McGraw & Furedi, 2005), deer are seed predators (Furedi & McGraw, 2004). Similarly, by providing the opportunity for the establishment of new populations, thrush dispersal also provides a way of escaping harvest. Harvesters return year after year to the same ginseng populations (McGraw, Souther & Lubbers, 2010), so dispersal and establishment of new populations in areas where ginseng no longer exists could mitigate the effect of harvest on ginseng metapopulations. Furthermore, the ability of thrushes to act as a primary disperser provides the greatest opportunity for ginseng to persist in the face of climate change effects. Longer dispersal movements via thrushes would provide a greater opportunity for gene flow between locally adapted populations (Souther & McGraw, 2011; Souther & McGraw, 2014), which may in turn enhance the ability of populations to persist in the face of climate change.

Acknowledgements

We would like to thank J. Chandler, M. Elza, and J. Turner for their help with camera set up, image collection, and aquarium observations and their feedback on the early version of this article. We thank the Tennessee Aquarium for the use of their facilities and care of the birds, in particular A. George and K. Calhoun for all of their assistance. Financial support was received from National Science Foundation Long Term Research in Environmental Biology Grant DEB-0613611 and DEB-1118702 (to J. B. McGraw).

Literature cited

- American Ornithologists' Union, 2012. The Code of Nomenclature and Check-List of North American Birds Adopted by the American Ornithologists' Union: Being the Report of the Committee of the Union on Classification and Nomenclature. Forgotten Books, New York, New York.
- Augsburger, C. K., 1984. Seedling survival of tropical tree species: Interactions of dispersal distance, light-gaps, and pathogens. *Ecology*, 65: 1705–1712.
- Barga, S. C. & S. B. Vander Wall, 2013. Dispersal of an herbaceous perennial, *Paonia brownii*, by scatter-hoarding rodents. *Écoscience*, 20: 172–181.
- Baskin, C. C. & J. M. Baskin, 2001. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, California.
- Betts, M. G., J. C. Hagar, J. W. Rivers, J. D. Alexander, K. McGarigal & B. C. McComb, 2010. Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecological Applications*, 20: 2116–2130.
- Brown, D. R., C. S. Strong & P. C. Stouffer, 2000. Movement and territoriality of wintering Hermit Thrush in southeastern Louisiana. *Wilson Bulletin*, 112: 347–416.
- Clark, C. J., J. R. Poulsen, B. M. Bolker, E. F. Connor & V. T. Parker, 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology*, 86: 2685–2694.
- Clark, C. J., J. R. Poulsen, D. J. Levey & C. W. Osenbuerg, 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist*, 170: 128–142.
- Clark, D. & D. Clark, 1984. Spacing dynamics of a tropical rainforest tree: Evaluation of the Janzen–Connell model. *American Naturalist*, 124: 796–788.
- Cousens, R., C. Dytham & R. Law, 2008. *Dispersal in Plants: A Population Perspective*. Oxford University Press, Oxford.
- Cruse-Sanders, J. M. & J. L. Hamrick, 2004a. Spatial and genetic structure within populations of wild American ginseng (*Panax quinquefolius* L., Araliaceae). *Journal of Heredity*, 95: 309–321.
- Cruse-Sanders, J. M. & J. L. Hamrick, 2004b. Genetic diversity in harvested and protected populations of wild American ginseng, *Panax quinquefolius* L. (Araliaceae). *American Journal of Botany*, 91: 540–548.
- Cutler, T. L. & D. E. Swann, 1999. Using remote photography in wildlife ecology: A review. *Wildlife Society Bulletin*, 27: 571–581.
- Division of Management Authority, 2012. U.S. exports of American ginseng 1992–2011. US Fish and Wildlife Service, Department of the Interior, Washington, DC.
- Engler, R. & A. Guisan, 2009. MigClim: Predicting plant distribution and dispersal in a changing climate. *Diversity and Distribution*, 15: 590–601.
- Fenner, M. (ed.), 2000. *Seeds: The Ecology of Regeneration in Plant Communities*. 2nd Edition. CAB International, Wallingford.
- Furedi, M. A. & J. B. McGraw, 2004. White-tailed deer: Dispersers or predators of American ginseng seeds? *American Naturalist*, 152: 268–276.
- Hackney, E. & J. B. McGraw, 2001. Experimental demonstration of an Allee effect in American ginseng. *Conservation Biology*, 15: 129–136.
- Hames, R. S., K. V. Rosenburg, J. D. Lowe, S. E. Barker & A. A. Dhondt, 2002. Adverse effects of acid rain on the distribution of the wood thrush *Hylocichla mustelina* in North America. *Proceedings of the National Academy of Sciences*, 99: 11235–11240.
- Howe, H. F. & J. Smallwood, 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13: 201–228.
- Hughson, D. L., N. W. Darby & J. D. Dungan, 2010. Comparison of motion-activated cameras for wildlife investigations. *California Fish and Game*, 96: 101–109.
- Illuz, D., 2011. Zoochory: The dispersal of plants by animals. Pages 201–214 in J. Seck & Z. Dubinsky (eds). *All Flesh is Grass: Plant–Animal Interrelationships*. Springer, Dordrecht.
- Izhaki, I. & U. N. Safriel, 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos*, 54: 23–32.
- Johannsen, K., 2006. *Ginseng Dreams: The Secret World of America's Most Valuable Plant*. University Press of Kentucky, Lexington, Kentucky.
- Jordano, P., 1987. Avian fruit removal: Effects of fruit variation, crop size, and insect damage. *Ecology*, 68: 1711–1723.
- Kartez, J. T., 1994. *A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland*. 2nd Edition. Timber Press, Portland, Oregon.
- Lambert, F. R., 1989. Pigeons as seed predators and dispersers of figs in Malaysian lowland forest. *Ibis*, 131: 521–527.
- Levey, D. J., 1987. Seed size and fruit-handling techniques of avian frugivores. *American Naturalist*, 129: 471–485.
- Lewis, W. H. & V. E. Zenger, 1982. Dynamics of American ginseng *Panax quinquefolium* (Araliaceae). *American Journal of Botany*, 69: 1483–1490.
- McGraw, J. B. & M. A. Furedi, 2005. Deer browsing and population viability of a forest understory plant. *Science*, 307: 920–922.
- McGraw, J. B., S. M. Sanders & M. E. Van der Voort, 2003. Distribution and abundance of *Hydrastis canadensis* L. (Ranunculaceae) and *Panax quinquefolius* L. (Araliaceae) in central Appalachian region. *Journal of the Torrey Botanical Society*, 130: 62–69.
- McGraw, J. B., S. Souther & A. E. Lubbers, 2010. Rates of harvest and compliance with regulations in natural populations of American ginseng (*Panax quinquefolius* L.). *Natural Areas Journal*, 30: 202–210.
- McGraw, J. B., M. A. Furedi, K. Maiers, C. Carroll, G. Kauffman, A. Lubbers, J. Wolf, R. C. Anderson, M. R. Anderson, B. Wilcox, D. Drees, M. E. Van der Voort, M. A. Albrecht, A. Nault, H. MacCulloch & A. Gibbs, 2005. Berry ripening and harvest season in wild American ginseng. *Northeastern Naturalist*, 12: 141–152.
- McGraw, J. B., A. E. Lubbers, M. Van der Voort, E. H. Mooney, M. A. Furedi, S. Souther, J. B. Turner & J. Chandler, 2013. Ecology and conservation of ginseng (*Panax quinquefolius*) in a changing world. *Annals of the New York Academy of Sciences*, 1286: 62–91.
- Meyer, G. A. & M. C. Witmer, 1998. Influence of seed processing by frugivorous birds on germination success of three North American shrubs. *American Midland Naturalist*, 140: 129–139.
- Ozinga, W. A., R. M. Bekker, J. H. J. Schaminée & J. M. van Groenendael, 2004. Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology*, 92: 767–777.
- Pearson, R. G. & T. P. Dawson, 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology & Biogeography*, 12: 361–371.

- Piper, J. K., 1986. Effects of habitat and size of fruit display on removal of *Smilacina stellata* (Liliaceae) fruits. *Canadian Journal of Botany*, 64: 1050–1054.
- Pritts, K. D., 2010. *Ginseng: How to Find, Grow, and Use North America's Forest Gold*. 2nd Edition. Stackpole Books, Mechanicsburg, Pennsylvania.
- Robbins, C. S., 2000. Comparative analysis of management regimes and medicinal plant trade monitoring mechanisms for American ginseng and goldenseal. *Conservation Biology*, 14: 1422–1434.
- Rusch, U. D., J. J. Midgley & B. Anderson, 2013. Rodent consumption and caching behavior selects for specific seed traits. *South African Journal of Botany*, 84: 83–87.
- Russo, S. E., S. Portnoy & C. K. Augspurger, 2006. Incorporating animal behavior into seed dispersal models: Implications for seed shadows. *Ecology*, 87: 3160–3174.
- Schmidt, V. & H. M. Schaefer, 2004. Unlearned preference for red may facilitate recognition of palatable food in young omnivorous birds. *Evolutionary Ecology Research*, 6: 919–925.
- Schupp, E. W., P. Jordano & J. M. Gómez, 2010. Seed dispersal effectiveness revisited: A conceptual review. *New Phytologist*, 188: 333–353.
- Sibley, D. A., 2000. *The Sibley Guide to Birds*. Knopf, New York, New York.
- Smith III, C. G., P. B. Hamel, M. S. Devall & N. M. Schiff, 2004. Hermit thrush is the first observed dispersal agent for pondberry (*Lindera melissifolia*). *Castanea*, 69: 1–8.
- Souther, S. & J. B. McGraw, 2011. Local adaptation to temperature and its implications for species conservation in a changing climate. *Conservation Biology*, 25: 922–931.
- Souther, S. & J. B. McGraw, 2014. Synergistic effects of climate change and harvest on extinction risk of American ginseng. *Ecological Applications*, 24(6): 1463–1477.
- Stiles, E. W., 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in Eastern deciduous forest. *American Naturalist*, 116: 670–688.
- Swann, D. E., C. C. Hass, D. C. Dalton & S. A. Wolf, 2004. Infrared-triggered cameras for detecting wildlife: An evaluation and review. *Wildlife Society Bulletin*, 32: 357–365.
- Thuiller, W., C. Alber, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes & N. E. Zimmermann, 2008. Predicting global change impacts on plant species distributions: Future challenges. *Perspectives in Plant Ecology, Evolution, and Systematics*, 9: 137–152.
- Trine, C. L., 1998. Wood thrush population sinks and implications for the scale of regional conservation strategies. *Conservation Biology*, 12: 576–585.
- Uriarte, M., M. Anciães, M. T. B. Da Silvia, P. Rubim, E. Johnson & E. M. Bruna, 2011. Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. *Ecology*, 92: 924–937.
- Vander Wall, S. B., 2010. How plants manipulate the scatter-hoarding behavior of seed-dispersing animals. *Philosophical Transactions of the Royal Society of Biological Sciences*, 365: 989–997.
- Vander Wall, S. B. & M. J. Beck, 2012. A comparison of frugivory and scatter-hoarding seed-dispersal syndromes. *Botanical Review*, 78: 10–31.
- Vander Wall, S. B., K. M. Kuhn & J. R. Gworek, 2005. Two-phase seed dispersal: Linking the effects of frugivorous birds and seed-caching rodents. *Oecologia*, 145: 282–287.
- Van der Voort, M. E., 2005. An ecological and demographic study of American ginseng (*Panax quinquefolius* L.) in central Appalachia. PhD thesis. West Virginia University, Morgantown, West Virginia.
- Vega Rivera, J. H., J. H. Rappole, W. T. McShea & C. A. Haas, 1998a. Wood thrush postfledging movements and habitat use in Northern Virginia. *Condor*: 100: 69–78.
- Vega Rivera, J. H., W. J. McShea, J. H. Rappole & C. A. Haas, 1998b. Pattern and chronology of prebasic molt for the wood thrush and its relation to reproduction and migration departure. *Wilson Bulletin*, 110: 384–392.
- Vega Rivera, J. H., W. J. McShea, J. H. Rappole & C. A. Haas, 1999. Postbreeding movements and habitat use of adult wood thrushes in Northern Virginia. *Auk*, 116:458–466.
- Vittoz, P. & R. Engler, 2007. Seed dispersal distances: A typology based on dispersal modes and plant traits. *Botanica Helvetica*, 117: 109–124.
- Wilson, D. E. & D. M. Reeder (eds), 2005. *Mammal Species of the World: A Taxonomic and Geographic Reference*. Johns Hopkins University Press, Baltimore, Maryland.
- Wheelwright, N. T., 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology*, 66: 808–818.