

## DOES HUMAN SCENT BIAS SEED REMOVAL STUDIES?

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**Abstract.** Field estimates of seed removal rates are often determined by monitoring the survival of seeds placed at stations. Such experiments may unintentionally provide seed predators with unnatural olfactory cues. We compared the removal of seeds that had direct contact with human skin (scented) vs. seeds that had no contact with human skin (unscented). At three Florida sites in 1997–1998, four to five species were tested by placing five conspecific seeds at each station; 40–50 stations per species, per treatment, per site were monitored for 30 d. Seed removal was greater for scented than unscented seeds, but most differences were significant only with all species and sites pooled. At two Illinois sites and one Florida site in 1999–2000, one seed of one of two species was placed at each of 400 stations and monitored for 30 d. Scented seeds were removed significantly faster than unscented seeds at Illinois sites (14% scented vs. 5% unscented removed after one day), but not at the Florida site. The effect of scent on removal was pronounced during the first week, then disappeared. Fortunately, these results suggest scent biases are weak and short-lived, and most studies are unaffected. Studies that may be affected are those of short duration.

*Key words:* experimental bias; granivore; olfactory cues; seed predation, seed removal.

### INTRODUCTION

Estimations of ecological processes are vulnerable to biases imposed by experimental design. For example, Cahill et al. (2001) found herbivory estimates were affected by the degree to which plants were handled during surveys. Field estimates of seed removal rates are often determined experimentally by placing seeds at stations and monitoring their survival. Using seed stations has allowed researchers to test hypotheses difficult to study using naturally dispersed seeds. Despite widespread use of seed stations, few studies discuss how accurately these experiments estimate natural seed removal or animal foraging patterns (Wenny 2002). Rodents are abundant seed predators in many systems and have an acute sense of smell (Vander Wall 1995, 1998). If researchers leave unnatural olfactory cues (e.g., human scent) on seeds, rodents may detect experimental seeds more than naturally dispersed seeds. This could lead to over- or underestimation of seed removal rates, depending on rodent response to these unnatural cues.

Similar studies of avian nest predation use artificial nests and/or artificial eggs to quantify egg predation (Major and Kendal 1996). Several studies have found higher predation rates on artificial than natural nests (Ortega et al. 1998, Sloan et al. 1998, Wilson et al. 1998, Rangen et al. 2000, Zanette and Jenkins 2000, but see Willebrand and Marcström 1988, Yahner and Voytko 1989, Skagen et al. 1999). Similarly, Whelan et al. (1994) found predation at artificial nests monitored by researchers wearing commercial deer scent (to mask unnatural odors) or scent-neutralizer was lower than predation at nests visited by researchers wearing perfume (a novel stimulus) or no scent manipulation. Human scent may also influence removal rates at experimental seed stations. We compared seed removal rates between seeds that had direct contact vs. no direct contact with human skin. Experiments were conducted in multiple forests in two geographic areas, using 10 species of vertebrate-dispersed seeds among 19 trials.

### MATERIALS AND METHODS

Initial seed removal experiments (experiment 1) were conducted in 1997–1998 at three forests in or near Gainesville, Florida (29° N, 82° W): Natural Area

Manuscript received 22 June 2001; revised 21 January 2002; accepted 21 January 2002.

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Teaching Laboratory (FL1) on the University of Florida campus, Paynes Prairie State Preserve (FL2), and San Felasco Hammock State Preserve (FL3). Secondary experiments (experiment 2) were conducted in 1999–2000 at two Illinois sites and one Florida site: Lost Mound National Wildlife Refuge (IL1) in northwestern Illinois (42° N, 90° W), Morton Arboretum (IL2) near Chicago (42° N, 88° W), and a dense successional forest (FL4) near Gainesville. Many seed predators occur at these sites, including 10–15 species of rodents in each geographic region.

Seed used in Florida included peppervine (*Ampelopsis arborea*), hickory (*Carya glabra*), flowering dogwood (*Cornus florida*), holly (*Ilex cassine*), poke-weed (*Phytolacca americana*), laurel cherry (*Prunus caroliniana*), cabbage palm (*Sabal palmetto*), and soapberry (*Sapindus marginatus*). At both Illinois sites, we used roughleaf dogwood (*Cornus drummondii*) and black cherry (*Prunus serotina*). Nomenclature follows Kurz and Godfrey (1993) for Florida and Mohlenbrock (1986) for Illinois. *Carya* is dispersed by tree squirrels, which often bury individual nuts (Koprowski 1994). The other species are dispersed by birds and mammals (Martin et al. 1951, Skeate 1987). The dispersal system of *Sapindus* is unknown. Mature fruits were collected directly from or below parent plants. Fruit pulp or husks were removed while wearing latex gloves rinsed in water (to reduce their scent). Seeds were then rinsed to remove residual pulp and husks. While odors from the pulp remained on the seeds, this processing mimicked the removal of pulp and husks from seeds when fruits are processed by vertebrate seed dispersers (a common procedure among seed removal studies). Seeds were then air-dried, sealed in plastic bags, and refrigerated until use. Throughout the process, contact between seeds and other materials (even gloved hands) was minimized, resulting in seeds that were cleaner than is typical of most experiments. To compensate for this and help ensure we put human scent on each seed, seeds for scent treatments were handled on the first day of an experiment. Hands were unwashed and manipulated seeds for one minute. After handling, scented seeds were probably typical of seeds used in most experiments. This procedure was done at all sites except IL2, where seeds were not handled extensively before being placed in the field.

For experiment 1, seed stations were set every 5 m along transects (but every 10 m at FL3). Each station was 1 m off the transects. Stations were small areas (<500 cm<sup>2</sup>) without leaves, and marked with 10-cm wooden stakes on the transect. Tops of the stakes were painted blue to aid relocation. Squirrels, the only local seed predators known to have color vision, seem unable to detect blue (MacDonald 1992, Koprowski 1994). A random species sequence was repeated along the tran-

sects to maximize distance between conspecific seed stations. Scented and unscented station order was determined randomly. For most species, five conspecific seeds were placed at each station. Small seeds (*Ilex*, *Phytolacca*, *Ampelopsis*) were placed in small petri dishes with holes. To simulate squirrel caches, *Carya* nuts were buried 1 cm deep, and 10 cm from an unpainted wooden golf tee, whose top was level with the soil surface. Before experiments, all materials left at stations, other than seeds, were rinsed in water, air-dried, and sprayed with a commercial scent-neutralizer (Scent-A-Way Human Scent Neutralizer, Hunter's Specialties, Cedar Rapids, Iowa, USA). While providing potential visual cues to predators, these materials were needed for relocating seeds on surveys.

Unscented seeds were placed at stations with forceps and rinsed latex gloves, and contact with other materials was avoided. Scented seeds were placed with bare, unwashed hands. When setting out seeds and during subsequent surveys, we wore rubber boots sprayed with Scent-A-Way. During surveys, rinsed latex gloves were worn, and when necessary, seeds were handled with rinsed forceps or twigs. Stations were checked 1, 3, and 7 d after deployment, when (if this scent fades) the human scent should be most detectable to predators. Seeds were then surveyed weekly for a month. When seeds were missing from a station, a 1 m diameter area around the station was searched; recovered seeds were put back on stations. Presence of *Carya* nuts was determined by probing the soil, though digging by predators was obvious when nuts were removed.

We did not use the same species at all three sites because 1) not all species occurred at each site, 2) seeds with very low removal rates at FL1 were dropped, and 3) small seeds used at FL1 and FL2 were too difficult to census after heavy rains. At FL1, each species had 40 stations per scent treatment (*Ampelopsis* had 37 unscented and 43 scented stations). Stations were set up the day before seed deployment. It rained on days 3, 4, and 13–15. Trials for *Ampelopsis* and *Phytolacca* were discontinued after heavy rain on day 4. At FL2 each species had 50 stations per scent treatment. Stations and seeds were set out on the same day. It rained on days 2, 6, 7, and twice during the remainder of the experiment. Trials for *Ampelopsis* and *Ilex* were discontinued after heavy rain on day 14. At FL3 each species had 50 stations per scent treatment. Stations were set up 11 d before seeds were set out. It rained on days 2, 3, 12, 21, and 22. During the last survey, some *Carya* seeds were rotting (10 scented, 7 unscented) and were excluded from analyses to avoid confounding scent treatments. The timing of trials for experiment 1 were as follows: FL1, November 1998; FL2, January 1998; and FL3, February 1998.

We modified the design for experiment 2 (IL1, IL2,

FL4) based on the results of experiment 1. Design improvements included 1) using one seed per station to avoid problems of multiple seeds per station, 2) increased sample size ( $N = 100$  per species per treatment), 3) reduced potential visual cues for predators, and 4) same species or genera used at each site. In experiment 2, two species were tested per site. Stations were 5 m apart, and species alternated along transects. Scent treatments were set on adjacent (10–15 m away) transects, because no evidence was found during experiment 1 of seed predators following transects. Potential visual cues were minimized by marking stations with twigs 10–15 cm away from stations (IL1 and FL4), or aged wood chips on transects. Stations were set 7–14 d before seeds were set out. Stations were checked at 1, 3, 7, 16, and 30 d. Experiments at IL1 and IL2 used *Prunus serotina* and *Cornus drummondii*, and started in October 1999. *Prunus caroliniana* and *Cornus florida* were used at FL4 in January 2000. No rain occurred at any site during experiment 2.

Removal rates at all sites were compared between treatments within each species using survival analysis and a Tarone-Ware test. This test compares differences in observed and expected survival times for all census intervals between two treatments (all analyses from SYSTAT 8.0; SYSTAT 1998). For stations with  $>1$  seed, a station “survived” until at least one seed was removed. Wald-Wolfowitz runs tests were used to look for serial removal of adjacent stations, which would suggest that seed predators followed transects. For experiment 1, the number of seeds removed per station was compared between treatments with Mann-Whitney  $U$  tests. Because removal events at stations were not necessarily independent, the number of stations with at least one seed removed was compared between treatments using Pearson’s chi-square test (or Fisher’s exact test if expected values were  $<5$ ). These analyses were conducted for data from day 1 and day 30, and post-hoc power analyses were computed. Survival analysis and log-linear models were used to analyze experiment 2. Because IL1 and IL2 ran concurrently and used the same species, data were combined for analysis (the unbalanced design of experiment 1 precluded log-linear models). Scent, species, and site were included in the model. The simplest log-linear model was estimated by specifying the full model (all main effects and higher order interactions), then removing terms not contributing significantly to the model. In this simplest model, predicted values do not differ from observed values ( $P > 0.05$ ). Terms retained contributed significantly ( $P < 0.05$ ), either directly or in an interaction (SYSTAT 1998). These analyses were performed separately for data from day 1 and day 30.

## RESULTS

With data from FL1, FL2, and FL3 pooled from experiment 1, more scented (6.4%) than unscented stations (4.0%) had at least one seed removed after one day of exposure (Pearson  $\chi^2 = 5.8$ ,  $df = 1$ ,  $P = 0.016$ ), but not at the end of the experiments (Pearson  $\chi^2 = 0.17$ ,  $df = 1$ ,  $P = 0.68$ ). Differences between scent treatments within species for having at least one seed removed were all nonsignificant, but of 13 individual trials, 11 had removal at more scented than unscented stations after one day of exposure (Table 1). This ratio is higher than expected if removal was the same for both treatments (sign test,  $P = 0.022$ ). At the end of the experiments, removal was similar for both treatments (sign test,  $P = 1.0$ ).

The total number of seeds removed per station at the end of day 1 was greater for scented than unscented treatments when data from all species and sites were pooled (Mann-Whitney  $U$  test,  $P = 0.008$ ). Only one of 13 trials within species had significantly higher removal at scented than unscented stations (Table 1), although 10 of 13 trials had more removal from scented stations (sign test,  $P = 0.092$ ). Total seed removal at the end of the experiments was not different between scented and unscented treatments when all species were pooled (Mann-Whitney  $U$  test,  $P = 0.53$ ), or when each species was analyzed separately (Table 1). The power of the analyses for individual trials ranged from 0.05 to 0.62, with 21 of 26 trials (13 for day 1, plus 13 for the end) having power  $<0.21$ . The low power resulted from small differences between treatments and fairly small sample sizes. For all sites and species pooled (bringing sample size per treatment to almost 600), power was 0.90 for day 1 and 0.13 for day 30.

The survival analyses indicated that the rates of seed removal from scented and unscented stations were similar for all species, except for *Cornus* at FL3, where scented stations had faster removal than unscented stations (Tarone-Ware  $\chi^2 = 4.7$ ,  $df = 1$ ,  $P = 0.03$ ). With data from all sites pooled, removal rates were similar for scented and unscented treatments (Tarone-Ware  $\chi^2 = 0.3$ ,  $df = 1$ ,  $P = 0.6$ ). The runs tests showed no indication that the fate (removal or no removal) of one station was related to the fate of adjacent stations after one day of exposure at FL1 ( $z = 1.2$ ,  $P = 0.2$ ) or FL3 ( $z = -0.97$ ,  $P = 0.3$ ). At FL2, however, seed removal after one day was significantly non-random ( $z = -4.8$ ,  $P < 0.001$ ). An examination of the raw data revealed four long runs of 66, 42, 69, and 39 consecutive stations with no removal, while almost 71% of removal occurred in two sections of the transect. The sections where seed removal was low corresponded to lengths of the transect with little understory vegetation, suggesting a habitat-dependent effect. These results sug-

TABLE 1. Seeds removed from stations with and without human scent during the first experiment.

Species	Time	No. of stations with removal			Seeds removed per station		
		Scented	Unscented	<i>P</i>	Scented	Unscented	<i>P</i>
FL1-Natural Area Teaching Laboratory							
<i>Ampelopsis</i>	day 1	3	5	0.46	0.3 ± 1.1	0.3 ± 1.0	0.50
	end	23	28	0.25	1.7 ± 2.0	2.2 ± 1.9	0.29
<i>Carya</i>	day 1	10	7	0.41	0.3 ± 0.4	0.2 ± 0.4	0.42
	end	39	40	0.31	1.0 ± 0.2	1.0 ± 0.0	0.32
<i>Phytolacca</i>	day 1	4	0	0.12	0.3 ± 1.1	0.0 ± 0.0	0.04
	end	16	13	0.48	0.1 ± 1.6	0.8 ± 1.5	0.38
<i>Sabal</i>	day 1	0	3	0.24	0.0 ± 0.0	0.2 ± 0.8	0.08
	end	32	36	0.21	2.7 ± 2.0	3.1 ± 1.9	0.36
<i>Sapindus</i>	day 1	5	1	0.20	0.3 ± 0.9	0.0 ± 0.2	0.08
	end	28	23	0.25	1.9 ± 1.9	2.0 ± 2.1	0.69
FL2-Payne's Prairie State Preserve							
<i>Ampelopsis</i>	day 1	9	6	0.40	0.7 ± 1.7	0.6 ± 1.6	0.40
	end	41	44	0.40	3.4 ± 2.0	3.2 ± 1.8	0.40
<i>Cornus</i>	day 1	10	6	0.28	0.7 ± 1.6	0.5 ± 1.4	0.28
	end	31	31	1.00	2.6 ± 2.4	2.5 ± 2.3	1.00
<i>Ilex</i>	day 1	2	1	1.00	0.1 ± 0.8	0.0 ± 0.1	0.56
	end	39	43	0.29	2.3 ± 1.9	2.6 ± 1.7	0.30
<i>Sabal</i>	day 1	4	3	1.00	0.4 ± 1.3	0.2 ± 1.0	0.70
	end	27	25	0.69	1.9 ± 2.3	1.9 ± 2.2	0.69
FL3-San Felasco Hammock State Preserve							
<i>Carya</i>	day 1	4	2	0.67	0.1 ± 0.3	0.1 ± 0.2	0.45
	end	31	28	0.83	0.7 ± 0.5	0.7 ± 0.5	0.84
<i>Cornus</i>	day 1	10	5	0.16	0.6 ± 1.5	0.4 ± 1.4	0.19
	end	44	42	0.06	3.7 ± 1.9	3.7 ± 1.9	0.29
<i>Prunus</i>	day 1	10	7	0.16	0.8 ± 1.8	0.5 ± 1.4	0.17
	end	41	40	0.14	3.7 ± 2.1	3.5 ± 2.1	0.06
<i>Sabal</i>	day 1	5	2	0.44	0.4 ± 1.2	0.0 ± 0.2	0.16
	end	28	39	0.02	2.0 ± 2.2	2.3 ± 1.8	0.88
All sites	day 1	76	48	0.02	0.4 ± 1.2	0.2 ± 0.9	0.008
	end	420	432	0.68	2.1 ± 2.1	2.0 ± 2.0	0.53

Notes: Scent treatments significantly affected only a few species, but pooled data show strong effects at day 1 of the experiment. "Removal" denotes  $\geq 1$  seed missing from station; number of seeds removed are means  $\pm 1$  SD.

gest that seed predators did not follow transects to find seeds.

In experiment 2, seed removal rates were higher for scented than unscented seeds with IL1 and IL2 combined (survival analysis; Tarone-Ware  $\chi^2 = 6.4$ ,  $df = 1$ ,  $P = 0.01$ ), but they did not differ between the two sites ( $\chi^2 = 0.001$ ,  $df = 1$ ,  $P = 0.9$ ; Fig. 1). Considering the sites separately, differences between the removal rates of scented and unscented treatments were marginally insignificant (IL1:  $\chi^2 = 2.8$ ,  $df = 1$ ,  $P = 0.091$ ; IL2:  $\chi^2 = 3.6$ ,  $df = 1$ ,  $P = 0.055$ ). At IL1, removal rates did not differ between scent treatments for either species (*Cornus*:  $\chi^2 = 0.65$ ,  $df = 1$ ,  $P = 0.42$ ; *Prunus*:  $\chi^2 = 2.4$ ,  $df = 1$ ,  $P = 0.12$ ), while at IL2, seeds with human scent were removed faster than unscented seeds for *Cornus* ( $\chi^2 = 9.05$ ,  $df = 1$ ,  $P = 0.003$ ), but not for *Prunus* ( $\chi^2 = 0.09$ ,  $df = 1$ ,  $P = 0.75$ ). At FL4, removal was very low and did not differ between scent treatments ( $\chi^2 = 1.39$ ,  $df = 1$ ,  $P = 0.23$ ) or species ( $\chi^2 =$

0.04,  $df = 1$ ,  $P = 0.83$ ), nor did removal differ between scent treatments within each species (*Cornus*:  $\chi^2 = 0.003$ ,  $df = 1$ ,  $P = 0.95$ ; *Prunus*:  $\chi^2 = 2.7$ ,  $df = 1$ ,  $P = 0.10$ ).

The log-linear analyses supported the survival analyses. The best model for day 1 at IL1 and IL2 combined included three main effects and two interaction terms (Table 2). This model indicates the proportion of seeds removed was higher for scented (0.14) than unscented (0.05) seeds, and was higher for *Cornus* (IL1 = 0.11, IL2 = 0.16) than *Prunus* (IL1 = 0.06, IL2 = 0.05). For removal at day 3 (not shown) the model was similar to that for day 1 with a significant effect of scent, but scent was not a significant predictor of removal in models for days 7 or 16 (not shown). The best model for removal by day 30 included only two significant interaction terms; the main effects retained were not significant, but were needed because of their inclusion in the interactions (Table 2). This model shows that the

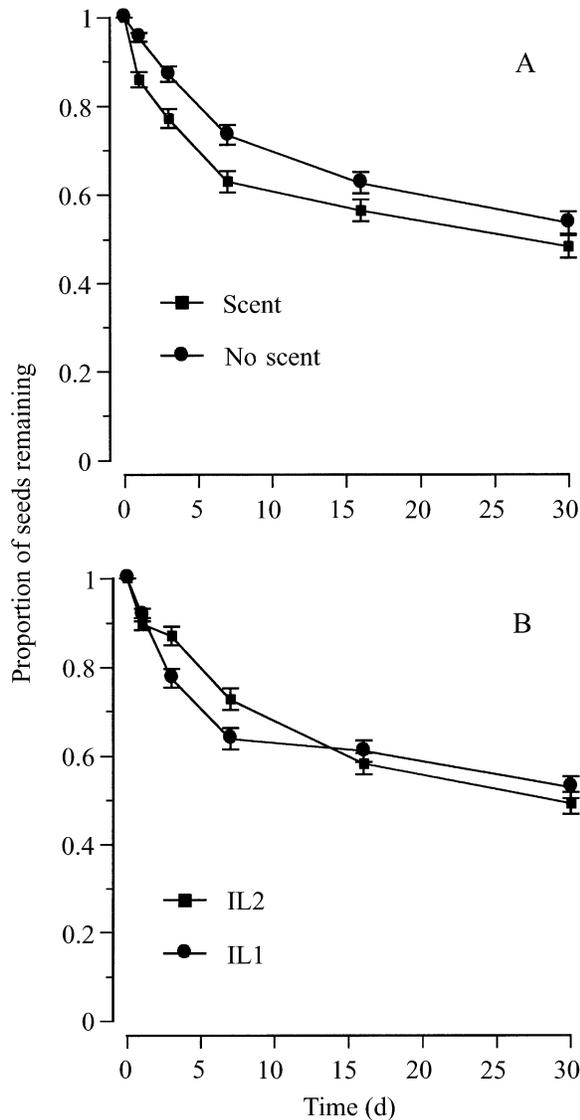


FIG. 1. Proportion of seeds remaining ( $\pm$ SE) at the two sites in Illinois in 1999 based on the Kaplan-Meier survivorship functions. Comparisons show survival of seeds (A) with human scent and with no scent for both species and sites combined, and (B) at the two sites for both treatments and species combined.

proportion of seeds removed was similar for scented and unscented seeds (0.52 and 0.46, respectively), and was higher for *Cornus* (IL1 = 0.50, IL2 = 0.60) than *Prunus* (IL1 = 0.48, IL2 = 0.38) overall. At FL4, no model fit the data for removal on day 1. For day 30, status (seed presence or absence) was the only term in the best-fitting model ( $G = 4.51$ ,  $df = 6$ ,  $P = 0.61$ ), and it was significant ( $G = 521.93$ ,  $df = 1$ ,  $P < 0.001$ ). This model showed that removal did not differ between species or treatments at FL4.

The runs tests indicated nonrandom removal at IL1 ( $z = -4.7$ ,  $P < 0.001$ ) and IL2 ( $z = -13.3$ ,  $P < 0.001$ ), but not at FL4 ( $z = -0.74$ ,  $P = 0.46$ ). The interpretation of these tests is more difficult than for the first experiment because the scent treatments were not randomized during the second experiment. Thus, if seed predators are attracted to unnatural scent, one would expect sequential removal in the second experiment. An examination of the raw data, however, suggests that habitat differences were at least as important as scent treatments. At IL1, which had parallel scent and no-scent transects, portions of the transects in treefall gaps with dense vegetation had higher removal than other areas, regardless of scent treatment. At IL2, removal appeared to be higher in an area of the forest with richer soils. At FL4, the lack of significant runs indicates low removal scattered throughout the transect.

#### DISCUSSION

Our results show that human scent on seeds can increase the probability of seed removal, but this effect is weak and short lived. This was found in several habitats of two geographic regions. Some individual trials showed significantly higher removal of scented than unscented seeds, suggesting the effect of human scent may be species dependent. But generally, a significant scent effect was found only when data from species and sites were pooled, and only for removal between one and three days of exposure. Removal was

TABLE 2. Best-fit log-linear models for experiments at IL1 and IL2.

Model and terms	$G$	df	$P$
Illinois day 1			
Overall model	3.74	10	0.958
Terms in model			
Scent	15.84	1	<0.001
Species	9.26	1	0.002
Status	640.27	1	<0.001
Scent $\times$ status	22.47	1	<0.001
Species $\times$ status	13.76	1	<0.001
Illinois day 30			
Overall model	8.20	10	0.609
Terms in model			
Location	0.13	1	0.718
Species	0.00	1	0.945
Status	0.32	1	0.568
Species $\times$ status	11.68	1	<0.001
Location $\times$ species $\times$ status	8.97	1	0.003

Notes: Variables include status (seed presence or absence), species (*Cornus* or *Prunus*), scent treatment (human scent or no scent), and location (IL1 or IL2). In each section the first item is the overall model where  $P$  indicates the probability the model fits the data. The following are terms in the model where  $P$  values  $< 0.05$  indicate that removal of the term from the model yields a poor fit to the data.

not consistently higher for either scent treatment after one week.

What is human scent and how long might it last? Human scent left on seeds touched with bare hands may be composed of secretions from sweat and sebaceous glands. While the components of sweat are water soluble and probably disappear rapidly with rain or dew (NaCl, KCl, urea, ammonia, lactate, proteins, and peptides; Olsen 1978, Demis 1986), sebum contains water-insoluble chemicals (e.g., glycerides, fatty acids, wax esters, and squalene; Barnhill 1998) that can persist for long periods (e.g., fingerprints). One interpretation of our results is that because the scent effect disappeared rapidly, seed predators may have been using components of sweat as a cue.

Fortunately, our results suggest most seed removal studies are unaffected by a scent bias because it is short lived and weak. However, there are several situations where such a bias may be important. First, studies of short-term processes (<1 wk) or studies in habitats where most seed removal occurs during the first days or hours (e.g., many tropical habitats) may be vulnerable. Second, scent bias may affect some seed species more than others, and the bias may interact with habitat. *Sabal* removal was greater for unscented seeds at the end of FL3, but not in FL1 and FL2. In addition, a concurrent seed removal study in Illinois, using the *Cornus* and *Prunus* species used in IL1 and IL2, found a much greater difference between scented and unscented treatments than we found (Wenny 2002). Third, scent bias can be important when comparing seed predators responding differently to human scent. Generally, our data suggest that the scent bias should not be of great concern to most researchers.

Few seed removal researchers report reducing scent cues left on seeds or seed stations. Typically, such precautions involve using gloves or forceps (e.g., Byrne and Levey 1993, Vander Wall 1998, Vander Wall and Joyner 1998, Wong et al. 1998). Others set up equipment at the study site prior to the experiments to let unnatural odors fade (Blate et al. 1998). In addition, most studies use visual cues that may bias results. It is much easier to criticize seed removal studies than it is to conduct them, and most of these criticisms apply to our own studies (Willson and Whelan 1990, Whelan et al. 1991, Wenny 1999, 2000, Duncan and Duncan 2000). We encourage other researchers to minimize unnatural cues available to predators, and to further investigate these and other potential biases.

#### ACKNOWLEDGMENTS

We thank Florida Division of Recreation and Parks, University of Florida Natural Area Teaching Laboratory Committee, and Morton Arboretum for site access. We thank G. Blate, C. Chapman, W. Gibbons, D. Levey, B. Molano-Flores, S. Moegenburg, J. Paul, A. Symstad, A. Zanne, and S. Brewer

for manuscript reviews. We thank University of Florida Department of Zoology, and Illinois Natural History Survey for supplies and support. This work was supported in part by a National Science Foundation Graduate Fellowship to R. Scot Duncan.

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