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Effects of weevil larvae on acorn use by blue jays

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Abstract Blue jays (*Cyanocitta cristata* L.) are important consumers and dispersers of the nuts of oaks and other fagaceous trees in eastern North America. Acorns compose much of the jay diet, especially during the autumn when jays may consume or cache a significant portion of an acorn crop. However, jays do not appear to possess physiological adaptations for countering the protein-binding properties of secondary compounds (tannins) found in acorns. We offered captive blue jays a mixture of infested and uninfested pin oak (*Quercus palustris* Muenchh.) acorns to see if the birds would selectively consume nuts containing weevil larvae (Coleoptera: Curculionidae) as a protein supplement to a high-tannin, all-acorn diet. Acorns were X-rayed to determine infestation status and then offered to individual jays in an outdoor aviary. Jays handled, opened, and consumed uninfested nuts significantly more often than infested nuts, and use of infested nuts did not increase during continued exposure to a high-tannin diet.

Key words Tri-trophic interactions · Oaks · Tannins · Blue jay · Weevils

Introduction

Increasingly, the role of “non-dispersing frugivores” (Herrera 1982, 1984; Ehrlen and Eriksson 1993) such as insects or microbes (Borowicz 1988; Buchholz and Levey 1990) that damage fruit or seeds is being considered in studies of fruit-frugivore interactions. The possible influence of infestation on fruit attractiveness to dispersing frugivores suggests that plant chemical defenses, fruit nutrient constitution, vertebrate frugivore nutrition and foraging behavior, and population dynamics of fruit-infesting organisms could interact to influence fruit seed dispersal (Scott and Black 1981; Herrera 1982; Manzur and Courtney 1984; Redford et al. 1984; Izhaki and Safriel 1989, 1990; Sallabanks and Courtney 1992; Valburg 1992a,b).

The relationship between acorns and jays may be influenced by similar interactions (Johnson et al. 1993). The blue jay (*Cyanocitta cristata* L.) may be a keystone species for recruitment of fagaceous trees in the eastern United States (Darley-Hill and Johnson 1981; Johnson and Adkisson 1985; Johnson and Webb 1989). Jays can consume a significant proportion of an acorn crop, but also cache a large number of acorns in the ground, providing long-distance dispersal (up to 4 km or more) and probably enhancing the potential for oak establishment (Bossema 1979; Darley-Hill and Johnson 1981; Johnson and Webb 1989).

Many acorn species appear to be “well-armed” with digestion-inhibiting secondary compounds called tannins (Ofcarcik and Burns 1971; Koenig and Heck 1988; Briggs and Smith 1989; Fleck and Layne 1990) that may bind up dietary protein, inhibit enzymatic activity, cause damage to the gut epithelia, or have direct toxic effects on herbivores (Butler et al. 1986; Robbins et al. 1987; Bernays et al. 1989). Like many species of fleshy fruits, acorns are also low in phosphorus and protein (Short 1976; Short and Epps 1976; Servello and Kirkpatrick 1987, 1989).

Although the bulk of the fall and early winter jay diet may consist of acorns (Beal 1896; Martin et al. 1951), jays appear unable to subsist for even a short time on an all-acorn diet in the laboratory (Koenig and Heck 1988; Johnson et al. 1993; Dixon et al. 1997). However, jays fed an adequate supplement of acorn weevil larvae (Coleoptera: Curculionidae) are able to maintain body mass on an otherwise all-acorn diet (Johnson et al. 1993). Acorn weevil larvae are abundant parasites or predators of acorns (Gibson 1982), and apparently reduce the num-

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ber of sound nuts for seedling establishment and wildlife food (Myers 1978). Given the availability of weevil larvae, the possibility that jays can distinguish between uninfested and infested nuts (Ligon and Martin 1974; Bossema 1979), and the need for jays to supplement their high-tannin acorn diets with high-protein food (Izhaki and Safriel 1989), weevil larvae could be a critical food resource for jays during acorn harvest and transport. If this is so, then low levels of weevil infestation may actually benefit oak populations in the long run by enabling jays to forage profitably on acorns and favoring long-distance dispersal of the remaining sound nuts (Johnson et al. 1993).

We investigated the possible influences of weevil infestation on jay foraging and acorn dispersal in an outdoor aviary. Our objectives were to determine: (1) the extent to which jays consume weevil larvae or other insects while foraging on acorns, (2) whether jays distinguish between infested and uninfested acorns for consumption and caching, (3) whether jays actively make use of a mix of infested and uninfested nuts during foraging, and (4) whether moderate levels of infestation may actually facilitate dispersal of the remaining sound acorns.

Methods

Diets of free-ranging jays

We examined stomach contents of wild jays to determine how frequently jays consumed weevil larvae or other arthropods during acorn harvest. Stomach contents were obtained by capturing and stomach-flushing wild birds, or by sacrificing wild birds and extracting the stomach.

Jays foraging in pin oak (*Quercus palustris* Muenchh.) trees in suburban Blacksburg, Virginia, were captured by placing elevated and ground-level mist nets between trees. Nets were set as high as 5.5–7.3 m above the ground by using telescoping aluminum poles (Meyers and Pardieck 1993) and were anchored using standards stabilized with guy wires and stakes. Nets were set out on several mornings during October 1993, when jay activity was highest.

Captured birds were induced to regurgitate stomach contents by flushing the stomach with a warm saline solution (Ford et al. 1982; Rosenberg and Cooper 1990; Major 1990). The solution was administered from a syringe and 4-mm tubing inserted down the esophagus of the bird. Some birds defecated during the flushing procedure. Regurgitation and fecal samples were placed in 10- to 20-ml vials containing ethyl alcohol as a preservative. Fourteen diet samples (from probably 14 different individuals) were obtained by stomach-flushing birds in the field.

We obtained additional stomach samples by sacrificing several wild jays that were foraging in oak canopies. Two jays were netted in Blacksburg and seven were collected at the Whitethorne Plantation Experimental Farm (near McCoy, Virginia), which is owned by Virginia Polytechnic Institute and State University. Stomachs were removed from the collected birds in the field, placed in alcohol, and put on ice.

Additionally, we fed weevil larvae to several captive birds, and then sacrificed one and stomach-flushed the others, to determine what weevil body parts were persistent and could be used to reliably detect the presence of the larvae in diet samples of wild birds.

Stomach contents were sorted in Petri dishes and examined with a dissecting microscope. Insect parts were separated and placed on slides using a mounting medium made of glycerol and gelatin (Davitt and Nelson 1980). Animal material was identified and quantified as the number of individuals per taxonomic group, down to order or family and to larval or adult stage for most arthropods. Acorn and other plant material was noted but not assessed quantitatively.

Behavioral trials in the aviary

Experiments to examine the response of jays to infested and uninfested acorns were conducted from September to November 1993 in an aviary facility on the Virginia Polytechnic campus. The 15 jays used in these behavioral experiments were captured in April and October 1993. Acorns of pin oak (*Q. palustris*), a member of the relatively high-tannin *Erythrobalanus* subgenus (Ofcarcik and Burns 1971; Koenig and Heck 1988; Briggs and Smith 1989), were used in all trials. Acorns were collected from trees and from the ground at various locations in Blacksburg.

Infested acorns were separated from uninfested acorns by a combination of flotation tests and X-rays (Semel 1984). Each acorn was marked with an identifying alphanumeric, using a fine point permanent marker. Infested and uninfested acorns were stored separately at 4°C until used in experiments. Most infested acorns contained weevil larvae (primarily *Curculio* but possibly some *Conotrachelus* weevils) and some contained moth larvae (probably *Valentinia glandulella* Riley; Williams 1989). Formerly infested acorns with larval exit holes and acorns containing the stone galls of cynipid wasps were discarded.

Trials in all experiments consisted of offering a jay a known mix of infested and uninfested acorns and recording its foraging choices. Each trial lasted 3–4 h. One morning (approximately 0800–1200 hours EST) and one afternoon trial (approximately 1400–1800 hours EST) were conducted each day. A trial was not officially begun until the bird handled one of the acorns, or until 15 min of observation had elapsed. During the morning trials, behavior and foraging choices by the jay were continuously monitored by an observer through a one-way mirror. In afternoon trials (which were not continuously monitored), jay foraging choices were determined by examining which acorns remained in the tray and which had been moved, opened, or consumed.

At the end of each trial, the whole acorns and fragments that had been handled by the jay were collected from the cage floor and identified. Acorns left on the tray were also identified. We recorded whether an acorn was opened, the approximate percentage of the endosperm that was eaten by the jay, and noted whether insect larvae were or had been present. Acorns with any part of the shell removed were considered “opened”. Acorns were designated as “eaten” if >10% of the endosperm was removed by the jay. In morning trials, acorns handled and taken to a perch were considered “taken,” whereas unopened acorns dropped off the tray were not. In afternoon trials, all acorns missing from the trays were considered “taken.”

In addition to the differences in protocol between morning and afternoon trials described above, additional alterations were implemented during a second set of experiments in the latter half of the season. Thus, four different experiments were conducted, divided by time of the day (morning or afternoon) and time during the season (phase 1 and phase 2). Morning trials (both phase 1 and phase 2) consisted of offering individual jays an equal mixture of infested and uninfested acorns, interspersed on a grid. Afternoon trials consisted of offering a jay acorns on two separate trays, with one tray containing only uninfested acorns and the other containing only infested acorns (phase 1) or a mixture of infested and uninfested (phase 2).

We were not interested in the effects of time of day on foraging choices, but wanted to keep variability within individual experiments to a minimum (because of small sample sizes), and wanted to test more than one hypothesis. Conducting one type of experiment only on mornings, and the other only on afternoons, meant that variability in bird behavior due to time of day would not be introduced in either experiment. Although activity patterns likely varied, we assumed that jay relative preference for infested or uninfested acorns did not vary according to time of day.

In experiment 1 (phase 1 morning trials), each jay was presented with a single tray with eight infested and eight uninfested acorns interspersed on a 16-cell grid. This experiment was designed to determine if jays could discriminate between infested and uninfested acorns in a mixture. Grid cells were delineated by a set of 2.5-cm-high cardboard dividers, on top of a 61×61 cm feeding tray. Acorns were assigned randomly to grid cells within the following restrictions: rows, columns and outer corners of the grid had to have equal representation of infested and uninfested nuts (two of each), and no more than three bordering cells (not including diagonal cells) could be of the same infestation status.

In experiment 2 (phase 1 afternoon trials), each jay was presented with two separate trays of acorns, one near the far left and one near the far right corner of the aviary (farthest from the observation window). Each tray contained 20 acorns, with one tray containing only infested acorns and the other containing only uninfested acorns. Acorns were simply spread out on the tray, with no grid divider. To avoid bias due to preference of the birds for one side of the aviary or one perch or tray to the other, assignment of infested or uninfested acorns to one tray or the other was alternated between consecutive trials. This experiment was designed to determine if jays preferred to forage from one source (location) or another depending on infestation status.

For the phase 1 morning trials, the bird was placed in the observation room the morning of the trial or the night before. In either case, food (e.g., dogfood) was available to the bird up until the beginning of the trial. Following completion of the morning trial, a new bird was moved to the central aviary cage and then deprived of food for 1–2 h before the afternoon trial was begun. Eleven birds were used for phase 1 trials, with each bird used for one morning and one afternoon trial (on different days).

As indicated above, we altered the protocol of morning and afternoon experiments during the phase 2 experiments (primarily in October 1993). For the morning experiment (experiment 3) we doubled the number of acorns (from 16 to 32) by adding another tray. This was done so that each jay would have more infested and uninfested acorns available than it was likely to handle during the 3- to 4-h experiment, since jays in experiment 1 sometimes exhausted the supply of uninfested acorns before completion of the trial.

In the afternoon experiment (experiment 4), we increased the number of acorns per tray from 20 to 30. Instead of having one tray with only infested acorns and one with only uninfested (as in experiment 2), we had one tray with all (30) uninfested nuts (100% uninfested) and one with 15 infested and 15 uninfested (50% infested). This experiment was designed to determine whether jays preferred to forage on a mixture of infested and uninfested nuts or on only uninfested nuts. We also wanted to determine if the presence of infested acorns increased or decreased the likelihood of the remaining uninfested nuts being taken.

A second adjustment in the phase 2 experiments was to use the same bird in consecutive morning and afternoon trials and to extend the trials to a second day. This was done because of concern that 3–4 h on an all-acorn diet may not have been enough time for a bird to experience the metabolic effects of high tannin intake. During longer exposure to an all-acorn diet, a bird might be more likely to experience a protein deficit and therefore be induced to seek supplemental protein. The extra time also furnished the opportunity for birds to “learn” about the availability of weevil larvae in the acorns as a possible protein source. Dietary stress should have been acute on the 2nd day, since birds in laboratory experiments lost considerable mass after just 2 days on an all-acorn diet (Johnson et al. 1993; Dixon et al. 1997).

In the phase 2 experiments, the bird was moved to the observation room the night before the trials, and all food was removed before dark. Beginning with the next morning’s trial, the bird was kept on an all-acorn diet until after the afternoon trial on the next day, and then was replaced with the next bird. Eight different birds were used in the phase 2 trials, with four newly captured birds and four birds reused from the phase 1 experiments.

Statistical analysis

Several different analyses were used to test for preference by jays for infested or uninfested acorns. All tests were two-tailed. Sign tests were used to determine if one type of acorn (infested or uninfested) was favored consistently across individual trials (birds) within experiments. Wilcoxon signed rank tests were applied in similar fashion, but were weighted by the magnitude of preference expressed by each bird for one acorn type or another. The absolute difference in the number of infested and uninfested acorns taken, opened, or eaten within each individual trial was used to determine ranking of preference in the signed rank test.

Chi-square goodness of fit tests were used to compare the total number of infested and uninfested acorns (pooled across individual birds/trials) taken, opened, or eaten within an experiment to that expected under the null hypothesis of no preference (equal numbers taken of each). In the case of phase 2 afternoon trials (experiment 4), comparisons were made between the total number of acorns handled (taken, opened, or eaten) from each tray (100% uninfested vs. 50% infested), the number of infested and uninfested acorns handled from the 50% infested tray, the proportion of uninfested acorns handled from each tray, and the proportions of uninfested and infested acorns handled overall, relative to the proportion of each presented (3:1 ratio of uninfested to infested). All chi-square statistics in goodness of fit tests were adjusted for continuity, using the Yates correction. Heterogeneity chi-square analysis was performed prior to pooling to test whether the individual samples (choices of individual birds) could be assumed to come from the same statistical population (Zar 1984).

Contingency table chi-square analyses were used to determine if proportional use of infested acorns differed between days 1 and 2 of the phase 2 trials, and to test for differences in the proportions of removed acorns that were opened and opened acorns that were consumed, according to infestation status.

Results

Jay diets

Acorn material was present in 83% (19 of 23) of the stomach contents of stomach-flushed and sacrificed wild jays (Table 1). Insect material (e.g., wings, legs, mandibles, other exoskeleton fragments) was found in 87% (20 of 23) of the samples. Animal remains included spiders, larval and adult Coleoptera (including adult acorn weevils), adult Lepidoptera, Orthoptera, Hymenoptera, Diptera, and the leg of a deer mouse (*Peromyscus* sp.). Several stomachs contained parts of snail shells.

We found no evidence of consumption of acorn weevil larvae by wild birds. In samples from captive birds fed larvae, mandibles appeared to be the most persistent and recognizable indicator of the presence of weevil larvae in the diet. Although some of the samples from wild birds contained evidence of beetle larvae, none had mouthparts that matched those of the acorn weevil larvae fed to birds in the laboratory (different shape and/or too large). There was also no evidence of lepidopteran larvae in any of the diet samples.

Overall, jay diets showed few patterns, apart from the ubiquity of acorn material and high insect diversity. There was no evidence of acorn weevil (*Curculio* or *Conotrachelus*) larvae in any of the stomachs of wild jays.

Acorn choice trials

Jays took, opened, and consumed as many or (more typically) more uninfested than infested acorns in all ten tri-

Table 1 Occurrence of taxa in diet samples of blue jays

TAXA OF DIET COMPONENTS		NO. OF DIET SAMPLES (n=23)
ANIMAL MATERIAL:		
Class Insecta		
Lepidoptera	Noctuidae (adult)	1
Coleoptera	Carabidae (adult)	2
	Scarabidae (adult)	1
	Tenebrionidae (adult)	1
	Curculionidae (adult)	3
	Total adult beetles	12
	Miscell. beetle larvae	6
Orthoptera (grasshopper)		3
Hymenoptera	Vespidae	10
Diptera	Mycetophilidae	1
Miscell. insect material		2
Class Arachnida		
Araneae (spiders)		5
Phylum Mollusca		
Gastropoda (snails)		6
Class Mammalia		
Rodentia	Cricetidae (*Peromyscus*)	1
TOTAL SAMPLES WITH ANIMAL MATERIAL		20
PLANT MATERIAL:		
Acorn material		19
Miscell. plant material		3
TOTAL SAMPLES WITH PLANT MATERIAL		20

Table 2 Totals and statistical comparisons of number of uninfested (*U*) and infested (*I*) acorns taken, opened, and eaten, in experiments in which equal numbers of uninfested and infested acorns were offered to the birds

EXPERIMENT		U	I	Sign test[a]	Signed rank[b]	χ^2 (1 *df*)
1	TAKEN	58	31	9,0*	45,0*	7.596*
	OPENED	46	19	8,0*	36,0*	10.400*
	EATEN	41	11	9,0*	45,0*	16.173*
2	TAKEN	118	43	11,0*	66,0*	34.012*
	OPENED	61	12	10,0*	55,0*	31.562*
	EATEN	54	7	11,0*	66,0*	34.689*
3	TAKEN	147	60	8,0*	36,0*	35.730*
	OPENED	107	31	8,0*	36,0*	40.761*
	EATEN	97	18	8,0*	36,0*	52.904*
4[c]	TAKEN	66	22	8,0*	36,0*	21.011*
	OPENED	54	11	8,0*	36,0*	27.139*
	EATEN	53	4	8,0*	36,0*	40.421*

*$P<0.01$

[a] Statistics for sign test: first number represents number of trials in which the number of uninfested handled exceeded the number of infested. The second number is the converse. Ties are excluded

[b] Statistics for signed rank test: the first number represents the rank sum, $T+$, for positive differences within trials (uninfested exceeded infested), the second number represents the rank sum, $T-$, for negative differences (infested exceeded uninfested)

[c] These totals represent the number of infested and uninfested acorns removed from the 50% weeviled tray in experiment 4

als of experiment 1 and all eleven trials of experiment 2. Pooled across the trials, 2–8 times more uninfested acorns were taken, opened, or consumed, than were infested acorns, in each experiment (Table 2).

Similarly, in experiment 3, more uninfested than infested acorns were taken, opened, and consumed by the jays in all eight trials and on each day. Pooled totals within and across days again differed significantly from a 1:1 ratio, with uninfested nuts preferred 2- to 5-fold (Table 2). Proportions of total infested to uninfested nuts removed, opened, and consumed did not differ significantly between 1st and 2nd days of the trials ($P>0.5$ for each), suggesting that relative preferences for uninfested and infested acorns did not change with longer exposure to an all-acorn diet.

In experiment 4, birds generally took more acorns from the 100% uninfested tray than from the 50% infest-

Table 3 Totals and statistical comparisons of numbers of acorns handled by jays, by infestation status and tray (100% uninfested and 50% infested trays) in experiment 4. (*Obs* the observed number of acorns handled in the trials, *Exp* the number expected, based on the proportion of infested, *I,* and uninfested, *U,* acorns presented, and the total number handled)

		Obs	Exp	χ^2 (1 *df*)
TOTAL ACORNS				
TAKEN	100%U tray	147	117.5	14.315*
	50%I tray	88	117.5	
OPENED	100%U tray	103	84	8.149*
	50%I tray	65	84	
EATEN	100%U tray	100	78.5	11.236*
	50%I tray	57	78.5	
UNINFESTED ACORNS				
TAKEN	100%U tray	146	141.33	0.369^{ns}
	50%I tray	66	70.67	
OPENED	100%U tray	102	104	0.065^{ns}
	50%I tray	54	52	
EATEN	100%U tray	99	101.33	0.100^{ns}
	50%I tray	53	50.67	
RATIO I/U OVERALL				
TAKEN	NO. INFESTED	23	58.75	28.200*
	NO. UNINFESTED	212	176.25	
OPENED	NO. INFESTED	12	42	27.627*
	NO. UNINFESTED	156	126	
EATEN	NO. INFESTED	5	39.25	38.694*
	NO. UNINFESTED	152	117.75	

*$P<0.001$, *ns* not significant

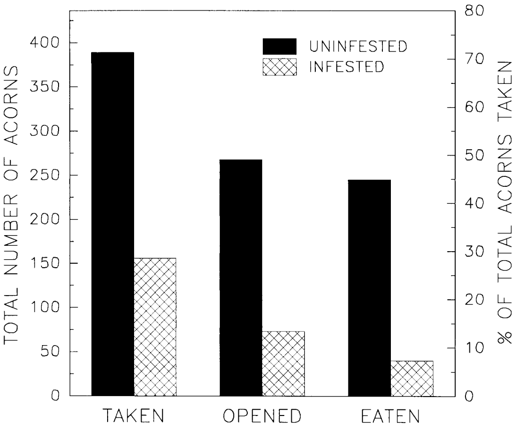

Fig. 1 Total number and proportion of uninfested and infested acorns taken, opened, and consumed, summed across experiments or trays in which uninfested and infested acorns were equally available

Table 4 Numbers and proportions of uninfested and infested acorns taken, opened, and eaten (includes data additional to that reported in the experimental trials). Percentages are based on the previous level of the hierarchy (opened/taken, eaten/opened)

	Uninfested	Infested
TAKEN	572	184
OPENED	398 (69.6%)	83 (45.1%)
EATEN	371 (93.0%)	48 (58.1%)
LARVAE MISSING	–	50 (60.2%)[a]

[a] Percentage of acorns with larvae missing is based on the number opened (missing/opened), not the number eaten

ed tray. However, such differences were generally either nonsignificant or marginally significant on both day 1 and day 2 of the trials. When the numbers are totaled across days within each trial, then acorns from the 100% uninfested tray were preferentially removed, opened, and consumed on seven of eight trials. Across trials, the total number of acorns removed, opened, and consumed was significantly greater for the 100% uninfested tray (Table 3). There was no significant change in tray preference between days one and two of the trials (*P*>0.5 for all).

The results of experiment 4 can also be partitioned in terms of actual numbers of uninfested and infested acorns taken, opened and consumed. Although significantly more uninfested acorns were handled from the 100% uninfested tray than the 50% infested tray, the total number of uninfested nuts removed from each tray did not differ significantly from a 2:1 ratio (Table 3), which is what would be expected on the basis of random sampling of uninfested acorns without respect to tray identity (30 uninfested acorns in the 100% uninfested tray, 15 in the 50% weevil-infested tray). Thus, infestation of the 50% weeviled tray did not seem to discourage (or encourage) the jays from foraging in that tray. Fewer uninfested acorns were removed from the tray primarily because there were fewer present.

In contrast, the proportion of infested nuts taken was far lower than expected at random (Table 3). The overall proportion of infested nuts available was 25%, but only about 10% of the nuts taken, 7% of the nuts opened, and 3% of the nuts eaten were infested. Within the 50% infested tray, greater numbers of uninfested than infested nuts were consistently removed, opened, and consumed (Table 2). Overall, few infested acorns were handled by the birds and very few were consumed.

Across all experiments, jays handled and removed, opened, and consumed uninfested nuts significantly more frequently than infested nuts (Tables 2 and 3). Overall, in experiments or trays in which uninfested and infested acorns were equally available, the ratio of uninfested to infested nuts taken was about 70:30 (Fig. 1), with the proportion of uninfested nuts progressively greater for opened and consumed acorns. Across all experiments, jays were more likely to open ($\chi^2=34.974$, 1 *df*, $P<0.001$) the uninfested nuts that were taken, and were more likely to consume a significant (>10%) proportion of the acorn material from the uninfested acorns that were opened than from the infested acorns

(χ^2=73.464, 1 *df*, *P*<0.001) (Table 4). Weevil larvae were missing and possibly eaten from a majority of the infested nuts that were opened. However, 40% of the infested acorns that were opened still contained at least one weevil or moth larva (Table 4), and this proportion would have been even higher had acorns that were punctured been included in the “opened” category.

Discussion

Overall, the jays in these experiments did discriminate between acorns based on infestation status, and preferred to handle, open, and consume uninfested acorns. Thus, the birds did not selectively consume weevil larvae to counterbalance the effects of high tannin intake. Indeed, the birds appeared to select against weevil-infested acorns, especially in terms of consumption, and did not increase relative consumption rates of infested acorns after more than a day on an all-acorn diet. Larvae that were present in opened acorns were often not eaten.

Jay behavior in the aviary suggested that the birds may have attempted to supplement their diet with protein from other sources. After eating several acorns, some birds began flying back and forth across the cage and appeared to search the corners, floor, and overhanging vegetation at the top of the aviary. Birds occasionally found and handled invertebrates, some of which did not appear to be very palatable (e.g., millipedes and hairy caterpillars that were often only partially eaten after considerable beating and handling by the bird).

Dietary samples from birds foraging on acorns in the wild showed no evidence of consumption of weevil larvae, but did show ubiquitous presence of acorns and of a diverse assortment of insect material. Evidence for consumption of adult wasps, grasshoppers, beetles (including a few adult acorn weevils), moths, spiders, a few non-*Curculio* beetle larvae, and even small mammal parts suggests that, apart from consumption of acorns, jays foraged opportunistically. Similarly, Beal (1896) found much variety in jay diets, but never mentioned consumption of acorn weevil larvae. Weevil larvae were also absent in the stomach contents of ten jays collected in Iowa (C. E. Williams, personal communication).

The scarcity of larvae in stomach samples may be due in part to high digestibility of the soft-bodied larvae, but larval mandibles proved to be fairly persistent and diagnostic of weevil presence in samples taken from birds fed larvae in the laboratory. However, absence of weevil larvae in a sample did not necessarily mean that they were absent from the diet. In flushings of laboratory birds, sometimes only a portion of what was eaten was recovered, and in some cases no larval parts were recovered. Actual stomach contents from birds sacrificed in the laboratory or field appeared to enable more complete reconstruction of the diet than did samples from stomach-flushed birds.

Although many studies have reported high levels of weevil infestation in acorn crops, few of the pin oak acorns found on the ground or on trees during the early part of the season (early to mid-September) were recognizably weevil-infested, and infestation rates in general appeared to be relatively low for pin oaks. A study in Missouri (Brezner 1960) also found low infestation rates for pin oak. Early stages of infestation also may have been difficult to detect via X-rays. Accuracy of X-ray differentiation between infested and uninfested nuts improved if nuts were kept in storage for a week or two, and most of the infested nuts used in our trials had probably been off the tree for as long as 2–3 weeks. A few acorns originally classified as uninfested were later found to contain larvae.

Our observations suggest that much of the weevil development occurred after acorn abscission. Indeed, premature abscission may be a defense mechanism for oaks and hickories (Myers 1978; Boucher and Sork 1979) in response to insect infestation. Jays will forage on the ground for acorns, but usually concentrate on acorns still on the trees until late in the season when most have fallen (authors’ personal observations; Vaughan 1991). Thus, the level of weevil biomass available to jays foraging in oak trees may be relatively low, even if a large percentage of the nuts are eventually infested.

Jays in our experiments may have assessed acorn quality in a hierarchical manner, using visual (acorn color), mass (acorn mass), tactile (flexibility of the shell), auditory (rattling the acorn in the bill), or gustatory (presence of frass or elevated tannin levels) cues, perhaps in that order. However, acorns that have been damaged in other ways, such as parasitism by stone gall wasps and fungal invasion, or that previously contained larvae that have since emerged, may provide a similar set of cues. These acorns may be moldy and/or filled with frass or may have elevated tannin levels as a result of damage (D. Fleck, personal communication). Thus, the cues that enable jays to discriminate between damaged and undamaged acorns may be unreliable for distinguishing acorns currently containing larvae from those that do not.

Even if jays did preferentially consume weevil larvae in the wild, it is doubtful that weevil larvae alone could supply enough protein to counterbalance the tannin intake from a high acorn diet. Opening an acorn takes time and energy, and the average cost for a jay opening an acorn that either contains a small larva or is empty and unpalatable may exceed the average gain (Semel and Andersen 1988). In the laboratory study by Johnson et al. (1993), 30–35 larvae per day was insufficient for birds to maintain mass on an otherwise all-acorn diet, while jays were able to maintain mass on a diet of approximately 110 larvae or 5 g per day. In a natural setting, where energetic demands and acorn intake would probably be higher, the number of larvae required to counter the effects of an otherwise all-acorn diet might be even greater. In contrast, opportunistic foraging on other, larger arthropods in the oak canopy or habitat at large may be less time-consuming and more efficient energetically than foraging selectively on the small weevil larvae, with fewer items and/or foraging bouts needed to supply the same amount of protein.

Thus, it may not be profitable for a jay to forage selectively on weevils, since weeviled acorns may be otherwise unpalatable (filled with frass); may have higher tannin levels in the remaining acorn endosperm (D. Fleck, personal communication); may supply relatively small amounts of larval biomass, protein, and energy (Semel and Andersen 1988); and may be unreliably distinguished from previously infested acorns that are empty (weevil has emerged and acorn is filled with frass) or that have been damaged or rendered unpalatable in some other way.

All in all, the interactions between jays and weevils appear to be relatively weak. This matches well with the conclusions of two recent studies on interactions between frugivores and pulp-mining insects (Traveset 1993; Traveset et al. 1995), but contrasts with several studies in which insect infestation enhanced the attractiveness of fruits to vertebrate frugivores (Scott and Black 1981; Redford et al. 1984; Valburg 1992a) and/or vertebrate frugivores were postulated to strongly affect populations of the infesting insects (Drew 1987; Herrera 1989). Weevil larvae may primarily affect jay-oak interactions by reducing the number of sound propagules available from the oak for consumption and dispersal by the jay. The ability of a jay to distinguish uninfested from infested acorns enables it to selectively forage on sound nuts or on nuts at early stages of infestation, and avoid acorns that have been severely damaged by weevils or by other causes. Benefit to the oak and the bird from weevil infestation of acorns is unlikely. Infestation reduces the number of sound propagules available to the oak (Myers 1978; Weckerly et al. 1989; but see Steele et al. 1993) and lowers the quality of the food resource for consumption and caching for the jay.

Thus, to answer our four original questions:

1. *To what extent do jays consume weevil larvae or other insects while foraging on acorns?* Stomach samples suggested that jays foraging in oak canopies consumed a diverse assortment of insects, but showed no evidence of consumption of acorn weevil larvae.
2. *Do jays distinguish between infested and uninfested acorns for consumption and caching?* Jays strongly preferred to take, open, and consume uninfested acorns over infested ones; however, caching behavior was observed too infrequently to yield any conclusions regarding acorn choices for caching. Evidence from other studies (Bossema 1979) suggests that jays prefer to transport uninfested nuts.
3. *Do jays actively make use of a mix of infested and uninfested nuts during foraging?* Jays consumed both infested and uninfested acorns, but strongly preferred uninfested acorns, preferred to forage from completely uninfested trays of acorns over mixed (uninfested and infested) trays, and did not appear to actively exploit infested acorns as a protein source, even under prolonged exposure to a high-tannin, all-acorn diet.
4. *Could moderate levels of infestation facilitate dispersal of the remaining sound acorns?* There was no sign of selective use of infested acorns and no evidence that the presence of infested nuts either increased or decreased use of surrounding uninfested nuts. Also, as mentioned previously, there were few observations of caching behavior in the experiments.

We emphasize that care should be taken in extrapolating the results of laboratory/aviary studies of animal behavior to conclusions about behavior of individuals in a natural setting. Particularly with an intelligent species that is sensitive to human presence, results in the laboratory could differ from those in the field. In our study, the artificial presentation of acorns and the absence of caching behavior in the birds limits the strength of our conclusions regarding the influence of weevil infestation on jay foraging and dispersal of oak propagules in the wild. Experiments in a more natural setting should be conducted to verify our aviary results.

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