Oecologia (1991) 86:402–407

Oecologia

Discrimination among pinyon pine trees by Clark's Nutcrackers: effects of cone crop size and cone characters

Kerry M. Christensen, Thomas G. Whitham, and Russell P. Balda

Department of Biological Sciences, Northern Arizona University, Box 5640 Flagstaff, AZ 86011, USA

Received January 17, 1990 / Accepted November 15, 1990

Summary. The influences of Colorado pinyon pine *(Pinus edulis)* cone crop size, cone and seed weight, cone length, number of seeds per cone, number of viable seeds, and percent viable seeds on the foraging behavior of avian seed dispersal agents were examined in field and laboratory settings. In the field, there was a significant positive relationship between cone number per tree and both the absolute number of cones and the percentage of the cone crop from which seeds were harvested. Cone weight and the number of viable seeds were also significantly related to seed harvest intensity. Laboratory experiments examined the relationship between crop size and cone characters on seed harvest by 18 Clark's Nutcrackers *(Nucifraga columbiana)*. Nutcrackers were offered a choice of two tree types: one with 20 cones attached, and another with 10 cones attached. Significantly more birds chose to remove seeds first from the tree with 20 cones than the tree with 10 cones. In timed trials, they also harvested seeds from significantly more cones on the tree with the higher cone density. In the laboratory, cones chosen for seed removal by the nutcrackers had significantly more viable seeds, more seeds, and were longer compared to cones that were not chosen. Such discriminatory foraging behavior may increase avian foraging efficiency and result in differential reproductive success of pinyon pines. This behavior may therefore influence the evolution of pinyon pine reproductive traits.

Key words: Pinyon pine reproduction – Discriminatory foraging behavior – Clark's Nutcracker – *Nucifraga columbiana* – *Pinus edulis*

The reproductive success of vertebrate-dispersed plants may depend not only on seed crop size (Herrera 1988) but also on the ability to attract seed dispersal agents (Howe and Primack 1975; Vander Wall and Balda 1977; Ligon 1978; Lanner and Vander Wall 1980; Clark and Clark 1981; Hutchins and Lanner 1982; Tomback 1982; Murray 1987). Many plant species exhibit significant intraspecific variation in both crop size (Linhart and Mitton 1985; Herrera 1988) and fruit or cone traits that attract dispersers (Howe and Estabrook 1977; Howe and DeSteven 1979; Howe and Vande Kerckhove 1979; Courtney and Manzur 1985). Because crop size and fruit traits have some genetic basis (Atsatt 1970; Atsatt and Strong 1970; Schaal and Levin 1976; Atsatt and Guldberg 1978; Paul 1978; Herrera 1981; Linhart and Mitton 1985) seed dispersers that discriminate among individual plants based on these characters may affect the evolution of these traits.

Pinyon pines depend on several birds in the family Corvidae for dispersal of seeds away from the parent to microsites that enhance germination probabilities (Vander Wall and Balda 1977; Ligon 1978). It is thought that seeds not dispersed away from the parent are lost to insect and rodent seed predators in most plants (Janzen 1970, 1972; Vander Wall and Balda 1977; Ligon 1978; Tomback 1982).

Clark's Nutcracker is an important disperser (along with the Pinon Jay, *Gymnorhinus cyanocephalus*) of Colorado pinyon pine seeds (Vander Wall and Balda 1977). Although these birds are also seed predators when foraging early in the day and season, and when harvesting small crops (Vander Wall and Balda 1977; Vander Wall 1988), they disperse seeds up to 22 km when harvesting larger crops. These birds have been found to effect forest regeneration (Tomback 1978; Ligon 1978; Lanner and Vander Wall 1980; Lanner 1980; Hutchins and Lanner 1982; Tomback 1982) due to their caching behavior, and have possibly been important to the range expansion of pinyon pines (Vander Wall and Balda 1977).

Previous studies have described apparent discrimination by nutcrackers among conifer stands (Tomback 1978), trees (Tomback and Kramer 1980; Benkman et al. 1984), and cones (Vander Wall and Balda 1977; Tomback and Kramer 1980), but have not examined in detail specific stand, tree, or cone characters influencing this

Offprint requests to: K.M. Christensen

discriminatory behavior. We examine the specific tree and cone characters that affect pinyon pine seed harvest by avian seed dispersal agents.

The question of why these birds discriminate among seeds, cones, and trees underlies each of these studies. Typically, foraging efficiency is invoked as the selective agent that has molded these behaviors (Vander Wall and Balda 1977; Tomback 1978; Tomback and Kramer 1980; Benkman et al. 1984; Vander Wall 1988). Presumably those individuals that maximized the amount of energy and/or nutrients gained per unit effort were most fit (Vander Wall and Balda 1977). While factors such as seed defense (Herrera 1982) and risk of predation (Howe 1979) may modify seed harvest behavior in birds, we feel that nutcrackers forage in a way that maximizes the rate of seed extraction. Below, we discuss how foraging on large crops may enhance nutcracker foraging efficiency.

To understand the factors influencing seed harvest of Colorado pinyon pine by Clark's Nutcrackers, we asked the following questions: 1) do differences in cone crop size and cone characteristics between trees in the field affect harvest intensity, 2) do nutcrackers choose trees for harvest based on crop size in a controlled laboratory setting?, and 3) do nutcrackers also discriminate among cones for seed harvest in the laboratory? The cone characters we examined included cone length, cone weight, seed number, number of viable seeds, percent viable seeds, and seed mass. These traits have been found to vary greatly among stands, trees, and cones (Vander Wall and Balda 1977; Christensen unpubl. data). Here we demonstrate that birds discriminate among trees based on crop size and cone characters.

Methods

In 1985, we measured cone number and subsequent seed harvest by nutcrackers and jays for 34 cone-bearing trees matched for trunk diameter at breast height near Sunset Crater National Monument, Flagstaff, Arizona. To determine crop size, cones were counted using the naked eye and/or binoculars in July just prior to the onset of avian harvest. We repeated counts on 10 trees and found that the counts were accurate within 5%.

We monitored seed harvest by nutcrackers and jays in late summer and fall from the beginning of harvest (18 July) until completion (30 September) at approximately 7 day intervals. These birds typically open green cones in a branch fork on the same tree from which the cone is removed (Vander Wall and Balda 1977). Removed cones were then counted in and under each tree. We cross-checked the number found with the number missing from each tree at each visit (also accounting for those consumed by rodents). If there was any discrepancy the tree was not used in the analysis (6 trees were not used). At our site, seeds were harvested from all but 2% of the cones before they opened, which made keeping track of harvest rates easier.

We used regression analyses (stepwise multiple regression; BMDP statistical package), with cone number per tree as the independent variable, to predict the absolute number of cones from which seeds were harvested and also the percentage of the cone crop from which seeds were removed. Percent crop harvest was arcsine square-root transformed prior to analysis.

To examine the influence of cone characters on seed harvest, we collected 20 closed cones from each tree prior to harvest initiation and measured, counted or calculated the following characters: cone length, cone weight (with and without seeds), seed number, number of viable seeds, percentage of viable seeds, and seed weight for each cone. These numbers were then averaged for each tree and used in a stepwise multiple regression analysis aimed at predicting the absolute number of cones and the percentage of the cone crop from which seeds were harvested. Although they are of normal size, non-viable seeds do not have a fully developed endosperm or embryo like viable seeds do, and often make up a large proportion of a tree's seed crop. Percent viable seeds was arcsine square-root transformed.

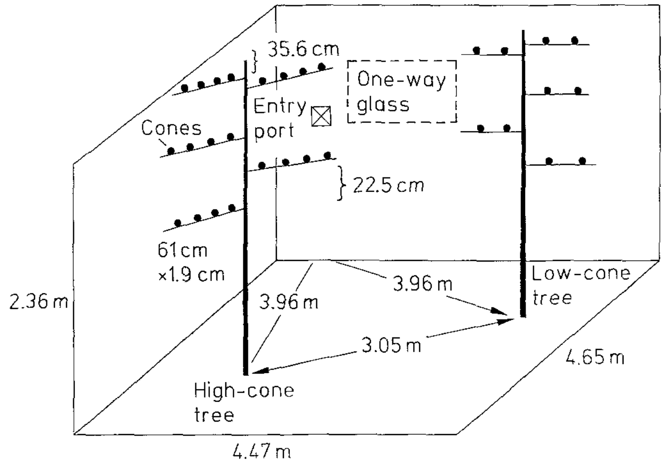

Fig. 1. A representation of the experimental room and artificial trees used in the nutcracker selection experiments

Laboratory experiments

In 1987, we conducted experiments in a room with two identical artificial trees. The physical characteristics of the room and the trees are depicted in Fig. 1. Twenty closed pinyon pine cones along with the subtending stem were collected from each of 8 haphazardly chosen trees in an area about 18 km north of Flagstaff. The cones were pooled, mixed, and used in the following experiments. We used 18 nutcrackers (14 recently caught and 4 that had been in captivity for approximately 2 years) in these experiments. The birds were fed and maintained as described in Kamil and Balda (1985).

Experiment I: effects of cone number on tree choice. This experiment tested the effect of relative cone number on a bird's initial choice of trees for harvest. We randomly selected twenty cones from the pool and attached to the branches of one tree (high-cone tree) using a piece of wire wrapped around the stem and the branch. Ten cones were then randomly chosen and attached to the other tree (low-cone tree). The cones were evenly spaced both within and among branches. A minimum of 10 cones was used because during preliminary trials it was determined that a single bird could not harvest seeds from more than 10 cones during the trial (50 min). This avoids the argument that the birds would harvest from more cones on the high-cone tree simply because there were more cones there to harvest. Furthermore, a two-fold difference in cone number is highly conservative because differences found between adjacent trees in the field may be more than 100-fold (Whitham and Mopper 1985). The tree that received the higher number of cones was determined by a coin toss before each trial.

Each nutcracker entered the experimental room alone. The birds were observed through a one-way glass observation port. Each bird was allowed to harvest from one cone on either tree as defined by the removal of one seed. We recorded the tree from which the first seed was harvested (high- or low-cone tree). We used the binomial

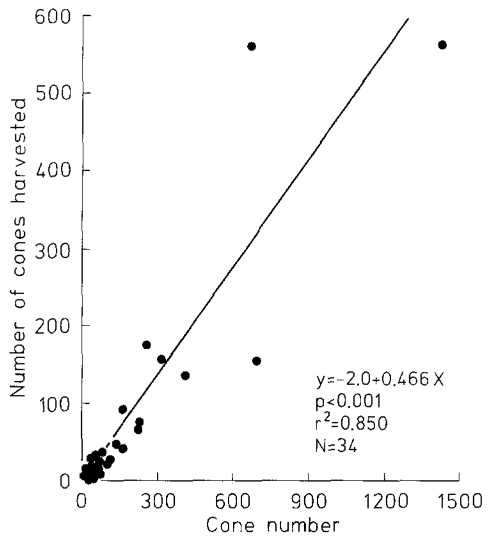

Fig. 2. Linear regression predicting the absolute number of cones from which seeds were harvested based on cone crop size of 34 adult trees

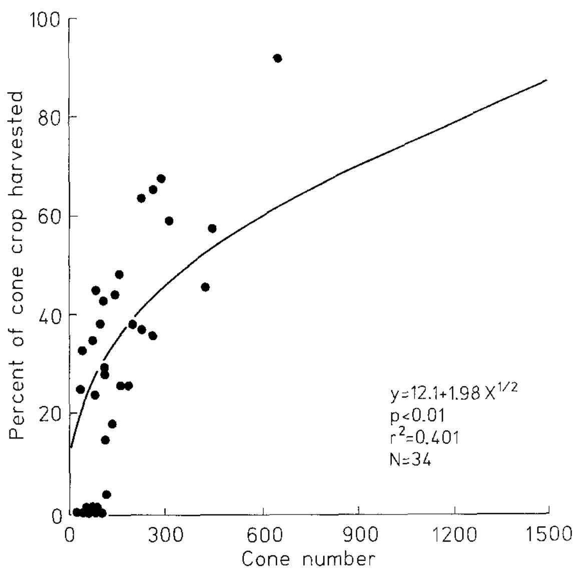

Fig. 3. Regression predicting the percentage of a tree's cone crop from which seeds were harvested based on cone crop size. The curvilinear line provided a significantly better fit than did a straight line (t = 4.47, $p < 0.05$)

test (Zar 1974) to determine if the number of cones had an effect on tree selection. The null hypothesis is that the birds should choose each tree in about one-half of the trials.

Experiment II: effects of cone number on harvest intensity. This experiment examined the effect of relative cone number on the number of cones from which seeds were harvested when we allowed the same birds to harvest for 50 min. Again, we attached 20 cones to one tree and 10 to the other, and the birds entered the room singly. We compared the mean number of cones opened from each tree in the 18 trials using the Wilcoxon Signed Ranks test (Conover 1980).

Results

Field observations

In the field, we found a significant positive relationship between cone crop size and the number of cones from which seeds were harvested (Fig. 2). This result agrees with other studies regarding the influence of crop size on seed harvest (Davidar and Morton 1986; Murray 1987), and demonstrates an advantage of greater seed production for plants.

The percentage of a tree's cone crop from which seeds were harvested by birds was also significantly affected by crop size (Fig. 3). This means that trees with larger cone crops have a greater proportion of their cones opened by birds, and should therefore realize greater relative fitness if seed dispersal is important to reproductive success.

Cone weight (without seeds) and the number of viable seeds were important in predicting the number of cones from which seeds were harvested (overall $r^2 = 0.363$, $p < 0.001$, $F = 16.93$, df = 2, 31; individual contributions to r^2 were 0.198 and 0.165 respectively). Thus, nutcrackers also selected trees based on these two cone traits. The reason why cone weight is important is unclear. Seed removal may be easier with heavy cones or it may simply be that cone weight is correlated with seed number ($r = 0.72$; Spearman rank correlation, $p < 0.05$). It is odd that both cone number and cone weight were more important in affecting tree choice than the number of viable seeds per cone.

The percentage of the crop from which seeds were harvested was also best predicted by cone weight and the number of good seeds (overall $r^2 = 0.365$; $p < 0.001$, $F = 17.20$, df = 2, 31; individual contributions to r^2 were 0.222 and 0.143 respectively). Again, in addition to cone number, nutcrackers also foraged selectively among pinyon pines by choosing trees with heavier cones with more viable seeds.

Laboratory experiments

Experiment I: effects of cone number on tree choice. In laboratory trials, nutcrackers were also very selective in their harvesting preferences; 13 of 18 birds harvested seeds first from the high-cone tree, allowing us to reject the null hypothesis the the birds would favor neither tree (Binomial test, $p = 0.03$). This result supports the hypothesis that cone number is very important in the selection of a tree for harvest even at a relatively fine scale (i.e. 20 versus 10 cones).

Experiment II: effects of cone number on harvest intensity. In 50 min trials, nutcrackers harvested seeds from more than 3 times as many cones from the high-cone tree than the low-cone tree ($\bar{X} = 2.47$ versus 0.78; Wilcoxon Signed Ranks test, $p < 0.001$, $n = 18$ pairs). Additionally, 10 of the 18 birds did not harvest any seeds from the low-cone tree, while all the birds harvested seeds from the high-cone tree. Thus, these birds not only chose the high-cone tree for initial harvest, but harvested seeds from more cones as well.

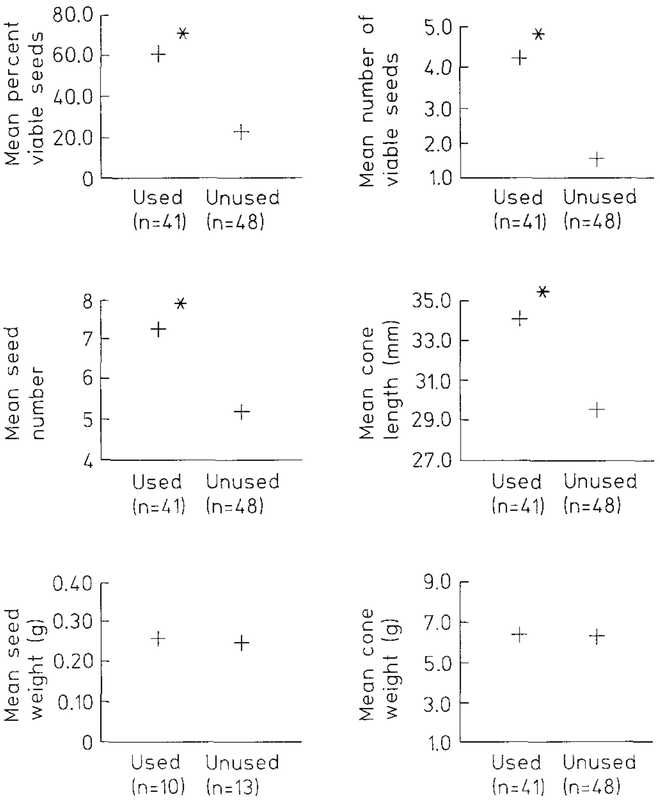

Fig. 4. Comparisons of the cone characteristics of those cones chosen and unchosen for seed harvest by nutcrackers in 50 min trials. Those with an asterik were significantly different in individual comparisons ($p < 0.05$)

The birds also harvested seeds from a significantly greater percentage of cones on the high-cone tree ($\overline{X} = 12.2\%$ versus 7.8%, Wilcoxon Signed Ranks. $p = 0.016$, $n = 18$ pairs). These results indicate that nutcrackers behaved similarly in the laboratory and the field, and attests to the strength of the influence of crop size on harvesting behavior.

Although nutcrackers discriminated among trees based on cone crop size, they also discriminated among cones within a tree. For example, cones from which seeds were harvested in the preceding experiment had on average 2.5 times the number of viable seeds, 40% more seeds, and were 15% longer than unchosen cones (Fig. 4; Hotelling's two-sample test, overall $p < 0.0001$). The cues used by nutcrackers to discern between cones with viable versus aborted seeds are unknown.

The cue(s) used by the birds to determine seed number is probably cone length. Seed number and cone length are significantly correlated (Spearman rank correlation, $r = 0.647$, $p < 0.01$); bigger cones have more seeds. It seems reasonable that a bird might first select the largest cones because they have the greatest potential energy payoff, and then sample smaller cones only if the larger cones contain few edible seeds.

Mean cone and viable seed weights were not significantly different between used and unused cones (Fig. 4). This result is different from what we found in the field where birds harvested seeds mostly from trees with heavier cones. It is possible that the birds behave differently when choosing between trees and when choosing between cones within a tree.

Discussion

These results show an increase in the absolute number of cones from which seeds were harvested with increasing cone crop size. Previous studies have found similar results in various seed dispersal systems; in absolute numbers, dispersers harvest more from plants with larger crops (Howe 1977, 1981; Howe and DeSteven 1979; Stapanian 1979; Moore and Willson 1982; Davidar and Morton 1986; Murray 1987). These studies, however, have generally found that the proportion of the crop harvested does not increase with increasing crop size (Howe and DeSteven 1979; Howe and Vande Kerckhove 1979, 1981; Moore and Willson 1982; Davidar and Morton 1986; Murray 1987).

The reason(s) why nutcrackers harvested a greater proportion of larger crops is unknown, but may relate to their foraging efficiency. By choosing trees with many cones, the birds may extract a greater number of seeds per unit time or energy. By having more cones to choose from, they may spend less time and energy handling cones with few viable seeds and traveling within and among trees. Other studies have suggested that these birds do forage in a manner that maximizes the efficiency of seed harvest (Vander Wall and Balda 1977; Tomback 1978; Tomback and Kramer 1980; Benkman et al. 1984; Vander Wall 1988).

For example, Vander Wall and Balda (1977) found that nutcrackers harvesting pinyon pine seeds were efficient seed collectors because they discriminated between viable and aborted seeds, selected cones with a higher than average number of good seeds, and "appeared" to concentrate on trees that produced cones with large numbers of good seeds. The results presented here confirm the preference of nutcrackers for trees and cones with many viable seeds and we propose that the birds chose to harvest from trees with many cones because it increased their harvest rates.

Tests of optimal foraging models (e.g. MacArthur and Pianka 1966; Charnov 1976; Pyke et al. 1977; McNamara 1982) are possible using nutcrackers foraging on pinyon pine. By recording travel, search, and handling times of foraging nutcrackers, and seed extraction rates, one might better understand how cone crop size truly influences foraging efficiency.

Although birds were observed transporting seeds away from the site where harvested, this and previous studies of avian harvest of pinyon pine seeds (Vander Wall and Balda 1977; Ligon 1978; Vander Wall 1988) have not determined the fate of harvested seeds. It was assumed that many of the seeds would be eaten by the birds themselves or by other seed predators. These studies estimated that in years of adequate seed availability nutcrackers and pinyon jays harvested, transported and cached many times the number of seeds needed for survival and reproduction. Many of the surplus seeds would therefore be available for germination. In light of the general belief that the birds are important to conifer reproduction (Vander Wall and Balda 1977; Ligon 1978; Tomback 1978; Lanner 1980; Lanner and Vander Wall 1980; Hutchins and Lanner 1982; Tomback 1982; Vander Wall 1988) and because birds were observed transporting seeds out of the study area, we argue that trees that received greater seed harvest also exhibited greater reproductive success.

The degree to which cone number, the number of viable seeds per cone, and cone size are genetically determined is of utmost importance to the argument that the birds have influenced the evolution of these traits. While no published data are available concerning the genetic basis of these characters in pinyon pine, at least fecundity has been shown to be genetically determined in other pines (Linhart and Mitton 1985) and in other plants (Paul 1978; Vander Kloet and Cabilio 1984).

Because there is a positive relationship between cone production and the percentage of a tree's seed crop dispersed, trees with larger crops receive a disproportionate return on their energy investment. This assumes that current reproductive effort has no impact on a tree's future survival or reproduction (Horvitz and Schemske 1988). While we do not know if this is true in pinyon pine, Linhart and Mitton (1985) found that current reproductive effort in ponderosa pine *(Pinus ponderosa)* did not reduce future effort. Selection should then favor those trees having greater fecundity (Herrera 1988), and there should be (or has been) an evolutionary trend toward greater investment in reproduction in pinyon pine. Vander Wall and Balda (1977) previously suggested that nutcrackers have affected the evolution of cone orientation, seed coloring, scale morphology, and seed retention of pinyon pine.

Acknowledgements. We thank J. Marzluff for advice concerning the design of the laboratory studies; J. Marzluff, M.E. Floyd-Hanna, S.B. Vander Wall, C.W. Benkman, J.H. Cushman, D.F. Tomback, and 3 anonymous reviewers for constructive comments on this manuscript. This work was supported by United States Department of Agriculture grants 84–CRCR–1–1443 and 87–CRCR–1–2361; National Science Foundation grants BSR–8705347 and BSR–8604983; a grant from Sigma-Xi, the Scientific Research Society; and a grant from the Arizona Wildlife Foundation.

References

Atsatt PR (1970) The population biology of annual grassland hemiparasites. II. Reproductive patterns in *Orthocarpus*. Evolution 24:598–612

Atsatt PR, Strong DE (1970) The population biology of grassland hemiparasites. I. The host environment. Evolution 24:278–291

Atsatt PR, Guldberg LD (1978) Host influence on floral variability in *Orthocarpus densiflorus* (Scrophulariaceae). Plant Syst Evol 129:167–176

Benkman CW, Balda RP, Smith CC (1984) Adaptations for seed dispersal and the compromises due to seed predation in limber pine. Ecology 65:632–642

Charnov EL (1976) Optimal foraging: the marginal value theorem. Theoret Pop Biol 9:129–136

Clark DA, Clark DB (1981) Effects of seed dispersal by animals on the regeneration of *Bursera graveolens* (Burseraceae) on Santa Fe island, Galapagos. Oecologia 49:73–75

Conover WJ (1980) *Practical Nonparametric Statistics*. Second edition. Wiley

Courtney SP, Manzur MI (1985) Fruiting and fitness in *Crataegus monogyna:* the effects of frugivores and seed predators. Oikos 44:398–406

Davidar P, Morton ES (1986) The relationship between fruit crop sizes and fruit removal rates by birds. Ecology 67:262–265

Herrera CM (1981) Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. Oikos 36:51–58

Herrera CM (1982) Defense of ripe fruit from pests: its significance in relation to plant-disperser interactions. Am Nat 120:218–241

Herrera CM (1988) The fruiting ecology of *Osyris guadripartita:* Individual variation and evolutionary potential. Ecology 69:233–249

Horvitz CC, Schemske DW (1988) Demographic cost of reproduction in a neotropical herb: an experimental field study. Ecology 69: 1741–1745

Howe HF, Primack RB (1975) Differential seed dispersal by birds of the tree *Caeseria nitida* (Flacourtiaceae). Biotropica 7:278–283

Howe HF (1977) Bird activity and seed dispersal of a tropical wet forest tree. Ecology 58:539–550

Howe HF (1979) Fear and frugivory. Am Nat 114:925–931

Howe HT (1981) Dispersal of a neotropical nutmeg *(Viola sebifera)* by birds. Auk 98:88–98

Howe HF, DeSteven D (1979) Fruit production, migrant bird visitation, and seed dispersal of *Guarea glabra* in Panama. Oecologia 39:185–196

Howe HF, Estabrook GF (1977) On interspecific competition for avian dispersers in tropical trees. American Naturalist. 111:817–832

Howe HF, Vande Kerckhove GA (1979) Fecundity and seed dispersal of a tropical tree. Ecology 60:180–189

Howe HF, Vande Kerckhove GA (1981) Removal of wild nutmeg *(Virola surinamensis)* crops by birds. Ecology 62:1093–1106

Hutchins HE, Lanner RM (1982) The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192–201

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528

Janzen OH (1972) Escape in space by *Sterculia apetala* seeds from the bug *Dysdercus fasciatus* in a Costa Rican deciduous forest. Ecology 53:350–361

Kamil AC, Balda RP (1985) Cache recovery and spatial memory in Clark's nutcracker *(Nucifraga columbiana)*. J Exp Psych: Anim Behav Proc 11:95–111

Lanner RM (1980) Avian seed dispersal as a factor in the ecology of limber and whitebark pines. Proc Sixth North Am For Biol Workshop, Univ. of Alberta, Edmonton, Alberta, Canada

Lanner RM, Vander Wall SB (1980) Dispersal of limber pine seeds by Clark's nutcracker. J For 1980, 637–639

Ligon JD (1978) Reproductive interdependence of pinyon jays and pinyon pines. Ecol Monogr 48:111–126

Linhart YB, Mitton JB (1985) Relationships among reproduction, growth rates, and protein heterozygosity in ponderosa pine. Am J Bot 72:181–184

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

McNamara JM (1982) Optimal patch use in a stochastic environment. Theoret Popul Biol 21:269–288

Moore LA, Willson MF (1982) The effect of microhabitat, spatial distribution, and display size on dispersal of *Lindera benzoin* by avian frugivores. Can J Bot 60:557–560

Murray KG (1987) Selection for optimal fruit-crop size in bird-dispersed plants. Am Nat 129:18–31

Paul NK (1978) Genetic architecture of yield and components of yield in mustard *(Brassica Juncea* (L.) Czern and Coss.) Theor Appl Genet 53:233–237

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. Quart Rev Biol 52:137–154

Schaal BA, Levin DA (1976) The demographic genetics of *Liatris cylindracea* (Michx. (Compositae)). Am Nat 110:191–206

Stapanian MA (1982) A model for fruiting display: seed dispersal by birds for mulberry trees. Ecology 63:1432–1443

Tomback DF (1978) Foraging strategies of Clark's nutcracker. Living Bird 16:123–161

Tomback DF (1982) Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. J Anim Ecol 51:1–46

Tomback DF, Kramer KA (1980) Limber pine seed harvest by Clark's nutcracker in the Sierra Nevada. Condor 82:467–468

Vander Wall SB, Balda RP (1977) Coadaptations of the Clark's nutcracker and pinon pine for efficient seed harvest and dispersal. Ecol Monogr 47:89–110

Vander Wall SB (1988) Foraging of Clark's nutcracker *(Nucifraga columbiana)* on rapidly changing pine seed resources. Condor 90:621–631

Vander Kloet SP, Cabilio P (1984) Annual variation in seed production in a population of *Vaccinium corymbosum*. Bull Torrey Bot Club 111:483–488

Whitham TG, Mopper S (1985) Chronic herbivory: impacts on architecture and sex expression in pinyon pine. Science 228:1089–1091

Zar JH (1974) Biostatistical Analysis. Prentice Hall