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ADAPTIVE GEOGRAPHIC VARIATION IN WESTERN SCRUB-JAYS

ELIZABETH BARDWELL,[1] CRAIG W. BENKMAN,[1,3] AND WILLIAM R. GOULD[2]

[1]*Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003-8001 USA*
[2]*University Statistics Center, Department of Economics, New Mexico State University, Las Cruces, New Mexico 88003 USA*

Abstract. Bill size and shape of Western Scrub-Jays (*Aphelocoma californica*) vary geographically in relation to habitat. Scrub-jays occupying pinyon–juniper woodlands (''pine'' scrub-jays) have relatively long, shallow bills, while scrub-jays occupying oak woodlands (''oak'' scrub-jays) have relatively stout, decurved bills. We captured five pine and five oak scrub-jays, and submitted them to feeding trials on pinyon pine (*Pinus monophylla*) cones and acorns (*Quercus agrifolia*) to determine whether geographic variation in bill structure was adaptive for foraging on these critical food resources. Three lines of evidence indicated that scrub-jays occuring in habitat dominated by either pinyon pine or oak had adaptive bill structure. First, scrub-jays exhibited a steep trade-off in feeding performance on pine cones and acorns. Pine scrub-jays extracted and consumed pinyon seeds more than 30% faster than did oak scrub-jays. Oak scrub-jays penetrated and consumed acorns twice as fast as pine scrub-jays did. Second, measures of feeding performance were moderately to strongly correlated with different measures of bill structure. Third, bill shape as measured by the ratio of bill length to depth was the metric that (1) best accounted for variation in feeding rates and (2) was related to the relative amount of pine and oak in habitats of 12 different populations of scrub-jays. These results, as well as others, were consistent with observed geographic variation in scrub-jays.

Key words: Aphelocoma californica; *ecomorphology; feeding performance; geographic variation;* Pinus monophylla; Quercus agrifolia; *trade-offs.*

INTRODUCTION

Studies of geographic variation have been a cornerstone to the development of evolutionary biology (Darwin 1859, Mayr 1963). The assumption that geographic variation is adaptive underlies these studies. For example, geographic variation in bill size and shape is thought to reflect variation in availability of different food resources to birds. This is often reasonable because bill structure determines its mechanical potential (Bowman 1961), which in turn influences feeding performance on a resource (Grant 1986, Grant and Grant 1989). Nevertheless, this assumption has been thoroughly tested and well supported in only a few cases (e.g., Grant 1986, Benkman 1993). Our goal was to test whether geographic variation in bill structure in Western Scrub-Jays (*Aphelocoma californica*) (hereafter referred to as scrub-jays), can be functionally related to geographic variation in food resources.

Scrub-jays are nonmigratory, and adults are territorial year round (Ritter 1983, Carmen 1988), making them likely candidates for adaptation to local conditions (Vander Wall and Balda 1981, Peterson 1990, 1993, Peterson and Vargas 1993). Recognition of several subspecies, based on geographic variation in morphometric and plumage traits, provides some evidence of local adaptation in scrub-jays (Pitelka 1951). These taxonomic distinctions are supported by protein electrophoresis studies that suggest limited gene flow between regional populations of scrub-jays (Peterson 1990). The two scrub-jay populations we sampled are separated by >100 km of the Mojave Desert, reducing the likelihood that gene flow constrains local adaptation (see Fig. 1; Peterson 1990, 1991). Conversely, the existing levels of gene flow reduce the chance that differences between subspecies are simply the result of drift (Peterson 1991).

In much of their range, scrub-jays occupy three principal habitats: pinyon, oak, and mixed pinyon–oak woodlands (Peterson 1993). Therein, bill size and shape are correlated with habitat (Peterson 1993). Scrub-jays in pinyon–juniper woodlands have shallow, straight, and pointed bills, while in oak woodlands their bills are relatively deep, decurved, and hooked (Fig. 1). Moreover, scrub-jays in different pinyon–juniper woodlands have independently evolved shallow, straight, and pointed bills from oak woodland ancestors two to four times (Peterson 1993). Differences in bill structure could be attributed to environmental effects. Environmental inducement of morphological change is prevalent in some taxa (e.g., fishes [Meyer 1987]), but has been documented only once in birds (James 1983). In most birds, bill size and shape are highly heritable (Boag and van Noordwijk 1987, Grant and Grant 1989). Although heritability of bill structure in scrub-jays has not been measured, two lines of evidence support a strong genetic basis for bill structure. One, the bill structure of four captive scrub-jays raised as nestlings

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[3] Corresponding author. E-mail: cbenkman@nmsu.edu

FIG. 1. Distribution of Western Scrub-Jays (in black; adapted from Peterson [1993]), the locations where scrub-jays were captured (at end of arrows), and representative scrub-jays and food resources used in the experiments. The scrub-jays depicted are representative of the typical bill structure found within each population and were traced from photographs. The open pinyon pine (*Pinus monophylla*) cone and seed (upper right) and coastal live oak (*Quercus agrifolia*) acorns (lower left) are drawn to relative scale (reproduced from Sudworth [1967]).

did not change in response to different diets over the duration of one year (Peterson 1993). Two, scrub-jays from oak woodland habitat that have recently invaded pinyon–juniper woodlands still retain a hook (Peterson 1993).

Pinyon seeds or acorns comprise 50–75% of the scrub-jay's diet during the fall and winter months, when most other resources are unavailable (Beal 1910, Bent 1946, Carmen 1988, Balda and Kamil 1989). Because of this seasonal reliance on seeds that mast some years, but are scarce in others, intense selection pressure could come to bear on bill traits affecting feeding performance on these seeds. Carmen (1988), for example, documented significantly higher mortality, reproductive failure, and territorial abandonment in scrub-jays during poor acorn years.

The different structure and size of pinyon seeds and acorns should favor different foraging behaviors and bill structures (Peterson 1993). Pinyon seeds have thin seed coats and are relatively small compared to acorns (Fig. 1), making them easier to husk and consume. However, pinyon seeds are retained in a protective cone that requires scrub-jays to reach between the open scales to extract seeds (Vander Wall and Balda 1981, Peterson 1993). Thus, a forceps-like bill, long, shallow, straight, and pointed, for probing, could be functionally advantageous to scrub-jays extracting pinyon seeds from cones (Peterson 1993), yet still suffice for removing the thin seed coat. A deep, decurved, or hooked bill, on the other hand, could interfere with seed extraction from a narrow scale opening (Peterson 1993). Acorns, in contrast, have thicker shells and larger kernels, making them relatively difficult to husk and consume without tearing and biting. There, a hooked bill could provide greater leverage for twisting and tearing off the shell (Peterson 1993), and a deep bill could withstand greater forces while pounding. Scrub-jays pound acorns with their lower mandible (Zusi 1987), but we assume bill depth is correlated with the pounding forces that the lower mandible can absorb. Further, a deep, relatively short, and decurved bill could exert greater biting forces at the tip (Grant and Grant 1989) for breaking off pieces of kernel, and the hook could exert greater leverage in removing these pieces. These functionally ideal forms are consistent with observed bill forms in scrub-jays occupying pinyon–juniper and oak woodland habitats.

Peterson (1993) made most of the above functional arguments to provide an adaptive explanation for the geographic patterns of bill structure variation in scrub-jays. However, Peterson did not test these functional arguments. Our research goal was to experimentally test the effect of morphology on feeding performance, and the functional basis of the adaptive hypothesis. Ideally, one would measure the relationship between morphology and fitness. However, measures of fitness are difficult to obtain. Arnold (1983) proposes separating the measurement of selection into (1) the effect of morphology on feeding performance and (2) the effect of feeding efficiency on fitness. The effect of morphology on performance can be measured in the laboratory, and in contrast to measurements of lifetime reproductive success or survivorship, is a relatively easy undertaking. Adopting Arnold's approach, measuring the effect of morphology on feeding efficiency would appear to be a critical and first logical step in substantiating or refuting an adaptive hypothesis of bill structure in scrub-jays (see Benkman and Miller 1996).

If geographical variation in bill form is adaptive, we predict two results. One, a trade-off in feeding performance will occur between the two populations of scrub-jays on the different resources. That is, scrub-jays from oak woodlands would have higher feeding rates on acorns than would scrub-jays from pinyon–juniper woodlands, and vice versa on seeds in pinyon pine cones. Otherwise, we would observe one generalist bill form across the populations rather than the observed geographic variation (Levins 1968). Two, specific bill traits, which should theoretically function better on a particular resource as described in the preceeding paragraph, will be positively correlated with feeding efficiency on that resource.

METHODS

Scrub-jay capture and care

We captured eight adult (after-hatch-year) scrub-jays of the subspecies *A. c. nevadae* (hereafter referred to as pine scrub-jays) in pinyon–juniper (*Pinus monophylla–Juniperus osteosperma*) woodlands in Mack Canyon, Spring Mountains, Clark County, Nevada, on 13 August 1998. Seven adult and one juvenile scrub-jay of the subspecies *A. c. obscura* (hereafter referred to as oak scrub-jays) were captured in southern oak (*Quercus agrifolia, Q. wislizenii, Q. chrysolepis,* and *Q. engelmannii*) woodlands located in the Santa Anita Drainage Basin, Arcadia, Los Angeles County, California, on 18–20 November 1998. Age was determined by plumage (Pyle 1997). Gender was not determined.

Scrub-jays were housed at the Animal Care Facility at New Mexico State University in cages that were 75 cm in length × 50 cm in width × 35 cm in height. We fed scrub-jays a mixture of sunflower seeds, parrot pellets, turkey starter, Purina bird chow, mealworms, and bird vitamins. In addition to the above, scrub-jays received five pinyon seeds inserted within open cones and two acorns per day while undergoing feeding experiments on pinyon seeds and acorns, respectively. Because scrub-jays would be released at the conclusion of the experiments, two scrub-jays at a time were allowed extended flight on a daily basis in a 3 × 3 m room, in order to reduce loss of breast muscle mass.

We excluded six scrub-jays from the analyses, three pine scrub-jays that broke off the tips of their lower mandibles while attempting to penetrate acorns, one oak scrub-jay that died early on during captivity, and two other oak scrub-jays (a juvenile and an adult with a crossed mandible) that could only forage marginally on either resource, or not at all. Thus, in most of the analyses, sample size was limited to 10 adult scrub-jays, five from each population.

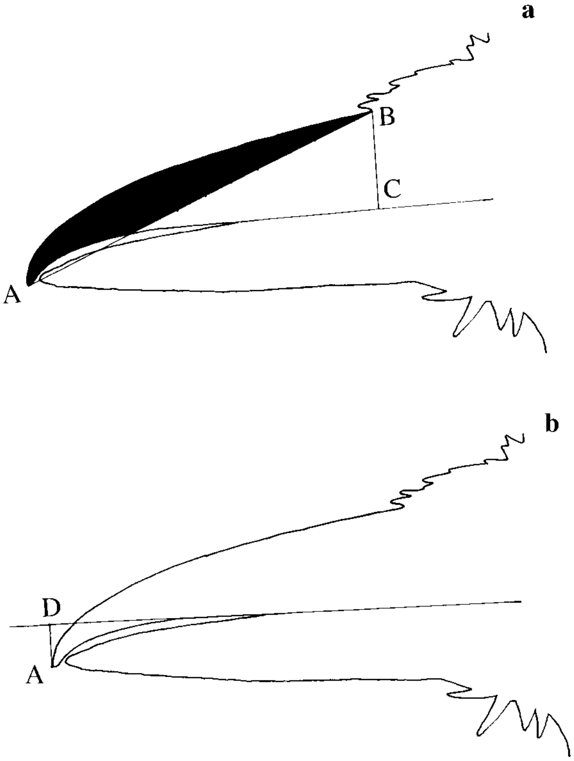

FIG. 2. (a) Curvature of culmen was measured as the ratio of area of the upper mandible occurring above the line drawn from the tip of the hook (A) to the distal tip of nasal feathers (B) (this area appears as the shaded section), over total area of the upper mandible as delineated by points A, B, and C. (b) Hook length was measured as vertical distance from the tip of the hook (A) to the intersection of the line (D) tangent to the tomia at the base of the bill.

Bill metrics

Five measurements characterized bill size and shape: length, depth, width, curvature of culmen (decurvature), and hook length. We measured bill length from the tip of the upper mandible to the anterior end of the nares. Bill depth and width were measured at the anterior end of the nares. Because bill length changed during captivity, we took measurements successively throughout captivity, (1) within 5 d of capture, (2) within 5 d of initiation of feeding trials, and (3) within 5 d of termination of feeding trials. We estimated bill length during a given feeding trial by averaging bill length at initiation and termination of the feeding trial. Bill depth and width were measured only once during captivity, as they were not expected to change. Bill length, depth, and width were measured to the nearest 0.01 mm using digital calipers. Repeatability of measurements (Lessells and Boag 1987) was as follows: 0.98 for bill length ($F_{29, 124} = 218.01$, $P < 0.001$), 0.94 for bill depth ($F_{9,35} = 74.2$, $P < 0.001$), and 0.85 for bill width ($F_{9,43} = 30.47$, $P < 0.001$). One of us (E. Bardwell) made all bill measurements.

We used image processing software, NIH Image, Version 1.6,[4] to measure curvature of culmen and hook length from photographs. Curvature of culmen was defined as the area of the upper mandible occurring above a straight line drawn from the tip of the hook to the distal tip of the nasal feathers, divided by the total area of the upper mandible (Fig. 2a). Hook length was defined as the vertical distance from the tip of the hook to a line horizontal with the tomium of the upper mandible (Fig. 2b). Photographs of scrub-jays were taken indoors using a FTb Canon camera with a 300-mm lens and three extension tubes totaling 68 mm for macro capability. We photographed scrub-jays at a standard distance of 108 cm from the lens, perpendicular to the camera. Photographs were digitized in Tagged Image File Format (TIFF) format using a Microtek ScanMaker III (Microtek, Redondo Beach, California) at 300-dpi optical resolution.

Photographs of scrub-jays were taken once within 5 d of initiation of feeding trials and once within 5 d of termination of feeding trials. We estimated curvature of culmen and hook length during feeding trials by

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[4] URL: ⟨http://rsb.info.nih.gov/nih-image/Default.html⟩

TABLE 1. Bill measurements at capture for eight pine scrub-jays and five oak scrub-jays.

	Pine scrub-jays			Oak scrub-jays	
Bill variable	$\bar{x}$	1 SE	P	$\bar{x}$	1 SE
Length/depth	2.50 (2.49)	0.05	<0.05	2.29 (2.16)	0.09
Length (mm)	20.46 (20.89)	0.19	0.34	20.15 (18.61)	0.71
Depth (mm)	8.11 (8.40)	0.11	0.001	8.82 (8.62)	0.16
Width (mm)	7.54 (8.00)	0.16	<0.05	8.23 (8.26)	0.26

Notes: In parentheses are the means from Pitelka (1951) for the subspecies in the area from which the experimental scrub jays were captured (weighted by sex, n = a total of 103 scrub jays). Comparisons were made using one-tailed t tests.

averaging curvature of culmen and hook length, respectively, at the initiation and termination of trials. Repeatability of measurements was as follows: 0.97 for curvature of culmen ($F_{38,39} = 67.91$, $P < 0.001$) and 0.96 for hook length ($F_{38,39} = 51.42$, $P < 0.001$).

Bill length changed during captivity. As a result, hook length, and to a lesser extent, curvature of culmen, also varied during captivity. We measured hook length and curvature of culmen only after changes had occurred in bill length. Hence, comparisons of bill metrics independent of changes during captivity could be made on only bill length, depth, and width, and possibly curvature of culmen.

Resources for feeding trials

Feeding trials were conducted on seeds of *Pinus monophylla* and *Quercus agrifolia.* Pine cones were collected from three trees in the Pine Nut Mountains, Nevada, on 7 September 1997. Cones were sorted into four size classes, with individual scrub-jays receiving ≥50% of trial cones from the two middle-size classes, in an attempt to standardize cone size. Green cones were dried at room temperature to initiate opening, and then stored in a freezer. Three days prior to each feeding trial, we removed experimental cones from the freezer. Seeds were removed, and the cones placed in a drying oven at 54°C for 40 h to harden pitch. After drying, cones were immersed in water for 10 min, and refrigerated in sealed plastic bags with approximately two tablespoons (~30 mL) of water for approximately eight hours, to facilitate closure of scales. During refrigeration, we placed a pinyon seed in each of two scales, on opposite sides in the upper half of the cone. One of two size classes of carpet tacks was then inserted at the distal end of the two scales in order to secure the desired gap opening. We inserted carpet tacks 6.0–7.0 mm in length to obtain 4.0–7.0 mm gaps (hereafter referred to as ''small gaps'') between the scales overlapping the seeds. We chose a gap size of 4.0–7.0 mm because it is shallower than the average bill depth of pine scrub-jays (see Table 1), making it relatively difficult to extract the seeds. Scrub-jays would not consistently forage on cones with only two small gaps, presumably because the cone was not ''open enough.'' Therefore, a third scale (without a seed) was opened in cones with small gaps, by inserting a 6.0–7.0 mm tack in the bottom half of each cone. To obtain a class of larger scale openings, we inserted carpet tacks 13.0–13.5 mm in length to obtain 8.0–13.0 mm gaps (hereafter referred to as ''large gaps'').

After refrigeration, we placed cones at room temperature, overnight, in a sealed plastic container until the next morning's feeding trials. At the time of trials, cones were screwed onto a 1.3-cm dowel, with scale openings aligned with the dowel when possible, and the dowel wedged inside the cage.

Acorns used in the experiments were collected from two trees in Santa Barbara County, California, on 24 September 1997. Acorns from the first tree (hereafter referred to as ''large acorns'') were on average wider (mean = 14.6 mm, 1 SD = 1.0, n = 50) than acorns from the second tree (hereafter referred to as ''small acorns'') (mean = 12.4 mm, 1 SD = 0.8 mm, n = 50). Only those acorns within one standard deviation of the mean diameter were used during feeding trials in an attempt to standardize acorn size. We froze acorns until the afternoon prior to feeding trials, at which time they were placed at room temperature overnight. Acorns were weighed to the nearest 0.1 mg on a digital scale immediately prior to trials. During feeding trials, we placed acorns on a wooden block (10 × 15 × 5 cm) within the cage, and we secured a 0.62-cm dowel on top of the block to provide a substrate on which scrub-jays could easily and repeatedly forage. After termination of a trial, the remaining acorn shell and kernel were removed from the cage, sealed in a plastic bag, and weighed to the nearest 0.1 mg with a digital scale, to determine the amount of kernel eaten.

Feeding trials

We allowed scrub-jays to forage on pine cones and acorns for at least one week before data collection. Timed feeding trials with pine scrub-jays and oak scrub-jays began 46 and 11 d after capture, respectively. We deprived scrub-jays of food for a minimum of 16 h prior to feeding trials, which were conducted between 0800 and 1030. Each scrub-jay underwent a maximum of two feeding trials per day, composed of two small-gap cones, two large-gap cones, or two acorns with one from each size category. During acorn trials, we altered the order in which the small and large acorns were provided, on a daily basis.

We reversed the order of food resources for pine and oak scrub-jays, with pine scrub-jays undergoing first pine cone, then acorn trials, while oak scrub-jays underwent first acorn, and then pine cone trials. Within pine cone feeding trials, the pine scrub-jays underwent feeding trials on small, then large gaps, while oak scrub-jays underwent feeding trials on large, and then small gaps. Feeding trials on pine cones lasted a total of 14 d for both pine and oak scrub-jays. Feeding trials on oak lasted a total of 13 d and 11 d for pine and oak scrub-jays, respectively. The reversal of feeding trials and gap size provided a conservative test of local adaptation, assuming feeding performance increased with time in captivity.

All feeding trials were videotaped and reviewed by one of us (E. Bardwell) to determine feeding times to the nearest 0.01 s. For feeding trials on pine cones, we recorded the time it took to extract and time it took to husk (i.e., to remove the seed coat and consume the kernel, which was consumed in its entirety after husking) each pinyon seed. For acorn feeding trials, we recorded the time it took to penetrate the shell and the time spent removing the kernel. Time to penetration began with the initial pounding of the acorn, and ended with the extraction and consumption of the first piece of kernel. Time spent removing kernel was the amount of time spent pounding, tearing off the shell, extracting, and eating the kernel within three minutes after penetration. We excluded time spent in other activities (e.g., scanning, moving around the cage) from the above recorded measurements. The mean number of trials per bird per resource type was 10 (range of 5–16).

We estimated feeding performance on pine cones by three parameters: time to extract a seed, time to husk a seed, and feeding rate (seeds/s). Feeding rate is the inverse of the time taken to extract and husk one pinyon seed. We combined seed husking times from cones with small and large gaps to estimate a mean seed husking time because we did not find, or expect to find, a significant difference in seed husking times between trials on cones with small and large gaps. We estimated feeding performance on acorns by three parameters, time to penetration, kernel removal rate after penetration (mg/s), and feeding rate (mg/s). Feeding rate is the amount of kernel eaten over the total time spent penetrating the shell and removing the kernel.

Partial correlation analyses

We used Spearman partial correlations to examine the relationship between an individual bill character and feeding performance, while controlling for other bill characters. Several bill characters exhibited colinearity with one another: bill width and depth ($r_s = 0.74$, $n = 10$, $P = 0.01$), and bill depth and curvature of culmen (during acorn trials, $r_s = 0.61$, $n = 10$, $P = 0.06$; and during pine cone trials, $r_s = 0.65$, $n = 10$, $P = 0.04$). To avoid problems with multicolinearity, three partial correlation models composed of the following bill characters were run: (1) bill depth, bill length, and hook length, (2) curvature of culmen, bill length, and hook length, and (3) bill length/depth and hook length. Bill width was not included in the analyses, because we did not predict an a priori functional hypothesis with respect to width and feeding performance. For the sake of simplicity, we report only the estimated partial correlation coefficients for bill length and hook length from the models using bill depth. Where the correlation coefficients for bill length and hook length derived from models using curvature of culmen and bill length/depth result in a more conservative test, we reference these results.

TABLE 2. Bill length (mm), curvature of culmen, and hook length (in pixels) during pine cone and acorn feeding trials.

	Pine scrub-jays			Oak scrub-jays	
Bill variables	$\bar{x}$	1 SE	P	$\bar{x}$	1 SE
Bill length					
Pine cone trials	21.27	0.29	<0.1	20.27	0.74
Acorn trials	21.10	0.25	>0.1	20.00	0.68
Curvature of culmen					
Pine cone trials	0.37	0.01	0.003	0.43	0.01
Acorn trials	0.35	0.01	0.001	0.43	0.01
Hook length					
Pine cone trials	1.46	0.16	>0.1	1.56	0.13
Acorn trials	1.27	0.09	<0.1	1.56	0.15

Notes: Sample size is 5 for both pine and oak scrub jays. Comparisons were made using one-tailed *t* tests.

RESULTS

Geographic variation in bill structure

Bill size and shape differed between the two groups of scrub-jays (Table 1). These differences were similar to those observed in a much larger sample of the same two subspecies, as reported by Pitelka (1951). Oak scrub-jays had significantly deeper and wider bills, and tended to have shorter bills than pine scrub-jays, although the difference in bill length was not significant nor as great as found by Pitelka (Table 1). Bill length changed during captivity, but it never differed significantly between the two groups (Tables 1 and 2). Oak scrub-jays also had stouter (lower values of bill length/depth, Table 1) and more decurved bills than pine scrub-jays (Table 2). In contrast to Peterson (1993), who found that scrub-jays from oak woodlands had longer hooks than did scrub-jays from pinyon–juniper woodlands, differences in hook length between the two groups during captivity were only marginally significant during feeding trials on acorns ($P = 0.066$, Table 2). Hook length did not differ significantly between the two groups during feeding trials on pine cones (Table 2).

Changes in bill length, however, may have influenced both curvature of culmen and hook length, neither of which were measured prior to changes in bill length. Therefore, we are unable to conclude whether oak

TABLE 3. Measures of feeding performance by oak and pine scrub-jays on pine cones.

Measure	Pine scrub-jays $\bar{x}$	Pine scrub-jays 1 SE	P	Oak scrub-jays $\bar{x}$	Oak scrub-jays 1 SE
Small gaps					
Extraction time (s)	8.16	1.64	>0.2†	10.79	3.14
Husking time (s)	33.75	3.12	0.13‡	46.32	6.74
Feeding rate (seeds/s)	0.024	0.002	0.03†	0.018	0.002
Large gaps					
Extraction time (s)	1.59	0.21	>0.2†	1.93	0.37
Husking time (s)	33.75	3.12	0.13‡	46.32	6.74
Feeding rate (seeds/s)	0.029	0.002	0.05†	0.022	0.003

Notes: Husking time for each population was averaged across both gap sizes and, as a result, is the same for both small and large gaps. Sample size is 5 for both pine and oak scrub jays.

† Comparisons were made using one-tailed *t* tests.

‡ Comparisons were made using two-tailed *t* tests.

scrub-jays had longer hooks than those of pine scrub-jays at time of capture. Differences in curvature between the two populations during captivity were highly significant, and probably were not an artifact of changes in bill length, because curvature of culmen was not correlated with upper mandible length (during acorn trials, $r_s = -0.02$, $P = 0.96$, $n = 10$; during pine cone trials, $r_s = 0.01$, $P = 0.99$, $n = 10$). Curvature was more strongly correlated with bill depth (during acorn trials, $r_s = 0.61$, $P = 0.06$, $n = 10$; during pine cone trials, $r_s = 0.65$, $P = 0.04$, $n = 10$), which did not change during captivity.

Feeding performance

As expected, pine scrub-jays tended to spend less time extracting and husking pine seeds and had significantly higher feeding rates on pine cones than did oak scrub-jays (Table 3). Oak scrub-jays required less time on average to penetrate acorn shells (significant only for small acorns), extracted kernel significantly faster once the shell was penetrated, and had significantly higher feeding rates on acorns than did pine scrub-jays (Table 4).

Foraging behavior and partial correlations between feeding performance and bill structure

Pine cones.—Scrub-jays with long, shallow, straight, and pointed bills should forage more efficiently on pine cones than scrub-jays with deep, decurved, and hooked bills. Bill shape, specifically the ratio of bill length to depth, explained more of the variation in feeding performance than did any of the individual bill characters alone (Table 5). Consistent with our predictions, scrub-jays with relatively long, shallow bills extracted seeds in less time and had significantly higher feeding rates (Table 5). Bill length was also positively and significantly correlated with feeding rates on cones with small and large gaps (Table 5). Bill depth was not significantly correlated with measures of feeding performance, although seed extraction time tended to increase with increasing bill depth, as predicted (Table 5). Hook length bore no correlation with extraction time and feeding rates (Table 5).

Table 6 provides a comparison of the predicted and observed relationships between bill characters and feeding performance on small-gap pine cones. Correlation coefficients derived only from an analysis of feeding performance on small gaps were used, because this is when differences in performance due to bill structure should be most pronounced. Limiting comparisons to cases where a positive or negative correlation was predicted, and assuming somewhat arbitrarily that r values $>|0.3|$ represent a positive or negative trend, the predicted trends were observed in five of the 10 cases.

TABLE 4. Comparisons between pine and oak scrub-jays on acorns.

Measure of feeding performance	Pine scrub-jays $\bar{x}$	Pine scrub-jays 1 SE	P	Oak scrub-jays $\bar{x}$	Oak scrub-jays 1 SE
Small acorns					
Penetration time (s)	74.27	11.06	<0.05	40.90	2.94
Kernel removal rate (mg/s)	2.8	0.4	<0.05	7.2	1.3
Feeding rate (mg/s)	1.7	0.3	<0.05	4.8	0.9
Large acorns					
Penetration time (s)	80.42	12.32	>0.1	61.80	7.23
Kernel removal rate (mg/s)	3.1	0.6	<0.01	6.7	0.6
Feeding rate (mg/s)	1.6	0.2	<0.01	3.5	0.5

Notes: Sample size is 5 for both pine and oak scrub jays. Comparisons were made using one-tailed *t* tests.

TABLE 5. Spearman partial correlation coefficients for bill characters and measures of feeding performance on pine.

Measure of feeding performance	Length/depth		Length		Depth		Curvature		Hook	
	r_s	P	r_s	P	r_s	P	r_s	P	r_s	P
Small gaps										
Extraction time	−0.52	0.07	−0.35	0.19	0.24	0.28	−0.16	0.65	−0.07	0.57
Husking time	−0.68	0.02	−0.69	0.06	0.15	0.72	0.25	0.55	0.02	0.96
Feeding rate	0.83	0.003	0.78	0.01	−0.36	0.19	−0.16	0.35	−0.05	0.45
Large gaps										
Extraction time	−0.44	0.12	−0.04	0.46	0.46	0.12	0.06	0.44	−0.01	0.51
Husking time	−0.68	0.02	−0.69	0.06	0.15	0.72	0.25	0.55	0.02	0.96
Feeding rate	0.68	0.02	0.69	0.03	−0.15	0.36	−0.25	0.27	−0.02	0.48

Notes: P values are one-tailed if the predicted relationship was negative or positive, but two-tailed if there was no a priori predicted relationship. Correlation coefficients for bill length and hook length were derived from partial correlations using bill depth. Correlation coefficients for length/depth were derived from partial correlations using hook length.

Acorns.—Scrub-jays with stout, deep, decurved, and hooked bills should forage more efficiently on acorns than scrub-jays with long, slender, straight, or pointed bills. As predicted, as bills became more stout, penetration time decreased and kernel removal rates and feeding rates increased (Table 7). Likewise, bill depth was negatively correlated with penetration time, and positively correlated with kernel removal rates and feeding rates (Table 7). These correlations were consistently significant on small acorns. Similarly, curvature of culmen was positively and significantly correlated with kernel removal rates on large acorns, and feeding rates on both small and large acorns (Table 7). Hook length should be correlated with kernel removal rates, but not penetration time, because scrub-jays spend relatively little time tearing off the shell, as compared to pounding prior to penetration. Hook length exhibited a moderate positive correlation with kernel removal rates on small acorns (Table 7), but as expected, was not correlated with penetration time.

Table 6 compares the predicted and observed relationships between bill characters and feeding performance on small acorns. Both bill depth and curvature of culmen are included in the comparisons, although they are highly collinear and may lack independence. Limiting comparisons to cases where a positive or negative correlation was predicted, and as before, assuming that r values $>|0.3|$ represent a positive or negative trend, the predicted trends were observed in all 10 cases (binomial test, $P < 0.001$). For large acorns, predicted trends were observed in nine out of 10 cases (binomial test, $P = 0.006$). Results differed slightly using the partial correlation coefficients for bill length and hook length derived from models using curvature of culmen; predicted trends were observed in nine of the 10 cases for small acorns (binomial test, $P = 0.006$) and eight of the 10 cases for large acorns (binomial test, $P = 0.03$).

DISCUSSION

Geographic variation in bill structure

We found patterns of geographical variation in bill structure similar to those in previous studies (Pitelka 1951, Peterson 1993). Pitelka (1951) examined bill length, depth, and width in the subspecies *A. c. obscura* and *A. c. nevadae*, which encompass the geographic ranges of our oak and pine scrub-jays, respectively. We both found that *A. c. obscura* had deeper, wider, and shorter bills than did *A. c. nevadae*. In addition, bill shape (bill length/depth) for each subspecies was similar to that found by Pitelka. Peterson (1993) examined

TABLE 6. Comparison of predicted (before slash) and observed (after slash) relationships between bill characters and measures of feeding performance.

Measure of feeding performance	Length/depth	Length	Depth	Curvature	Hook
Pine cones with small gaps					
Extraction time	−/−	−/−	+/0	+/0	+/0
Husking time	0/−	0/−	0/0	0/0	0/0
Feeding rate	+/+	+/+	−/−	−/0	−/0
Small acorns					
Penetration time	+/+	0/0	−/−	0/−	0/0
Kernel removal rate	−/−	0/0	+/+	+/+	+/+
Feeding rate	−/−	0/0	+/+	+/+	+/+

Notes: Partial correlation coefficients of 10.301 or higher were considered strong enough to represent a linear relationship with a nonzero slope. The − and + symbols indicate that the relationship is negative or positive, respectively. A zero indicates no a priori predicted or observed relationship.

TABLE 7. Spearman partial correlation coefficients for bill characters and measures of feeding performance on acorns.

Measure of feeding performance	Length/depth		Length		Depth		Curvature		Hook	
	r_s	P	r_s	P	r_s	P	r_s	P	r_s	P
Small acorns										
Penetration time	0.67	0.02	0.07	0.87	−0.66	0.04	−0.43	0.29	−0.29	0.48
Kernel removal rate	−0.68	0.02	−0.15	0.73	0.62	0.05	0.60	0.06	0.60	0.06
Feeding rate	−0.65	0.03	0.04	0.92	0.70	0.03	0.65	0.04	−0.36	0.19
Large acorns										
Penetration time	0.46	0.11	0.12	0.78	−0.16	0.35	−0.01	0.98	−0.21	0.62
Kernel removal rate	−0.62	0.04	0.12	0.78	0.78	0.01	0.69	0.03	0.39	0.17
Feeding rate	−0.67	0.02	−0.08	0.86	0.47	0.12	0.66	0.04	−0.38	0.18

Notes: P values and correlation coefficients were derived as in Table 5.

bill length, depth, and width, curvature of culmen, and hook length in several populations of scrub-jays occupying oak and pine woodlands. He found oak scrub-jays had significantly deeper and wider bills, and greater decurvature, and longer hooks than did pine scrub-jays, in at least one of the sexes. With the exception of hook length, our findings were similar. Peterson may not have detected significant differences in bill length because he sampled more widely, and included populations (more than one subspecies for each habitat type) that varied substantially in bill length. We might not have detected a significant difference in bill length because of our small sample sizes, and perhaps because of seasonal differences in bill length arising from differential wear. In the aviaries, we found that bill and hook length varied in response to foraging substrates. This suggests that bill and hook length may vary with seasonal differences in diet (see Peterson 1993, see also Davis 1954, Gosler 1987), so the extent of differences between populations may vary seasonally in the wild. Because we did not measure hook length at capture, the similarities in hook length between the two populations may reflect relatively greater growth of hook length during captivity in the pine scrub-jays or, alternatively, a seasonal affect. Our pine scrub-jays were captured in early August, while oak scrub-jays were captured in late fall when bills are more pointed (Peterson 1993).

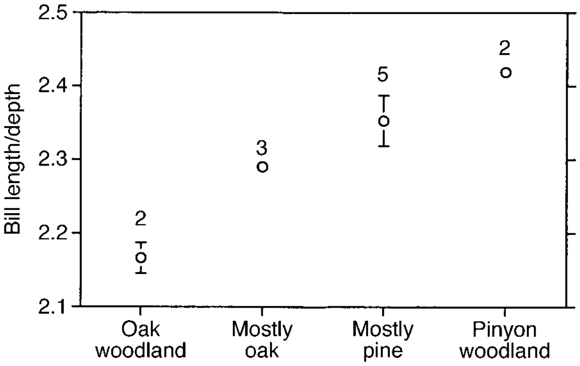

FIG. 3. Bill length/depth (mean ±1 SE) in relation to habitat. ''Mostly oak'' and ''mostly pine'' were mixed oak and pinyon pine habitats dominated by oak and pine, respectively. We used the mean, weighted by sex, for each population or geographic location in Peterson (1993) to estimate the mean and standard error for each habitat (data from Table 1 in Peterson [1993]; only samples including data for both males and females were used). The number of populations is given above each symbol. The standard errors cannot be seen for two of the habitats because they are smaller than the symbols for the means.

In summary, the pine and oak scrub-jays used in this study were representative in bill size and shape of the subspecies from which they were captured. The pine and oak scrub-jays used also represented well the bill sizes and shapes of other scrub-jay populations in pinyon–juniper and oak woodland habitats, respectively. The metric that best captured the differences between scrub-jays in habitats dominated by either pinyon pine or oak was bill length/depth. Scrub-jays in pinyon–juniper woodland have relatively large values of bill length/depth or long, shallow bills, compared with scrub-jays from oak woodlands (Fig. 3). Moreover, bill length/depth is the one metric for which scrub-jays from habitats containing a mixture of pinyon pine and oak are intermediate (Fig. 3).

Trade-off in feeding performance

Pine and oak scrub-jays exhibited a trade-off in feeding performance (Fig. 4). They differed consistently and significantly in the various measures of feeding performance on pine cones and acorns as predicted, with the exception of seed extraction time on pine cones, and penetration time on large acorns. This suggests that geographic variation in bill structure in scrub-jays is adaptive.

Failure to detect a significant difference in extraction time between the two groups may be an artifact of the experimental design. For example, we were only able to control the width of the gap between scales within certain bounds, and were unable to control for other features of the gap opening that could potentially influence extraction time, such as the patterning of scale overlap. Although this should not affect overall mean extraction times, it increases the variance (e.g., the coefficient of variation for seed extraction time averages

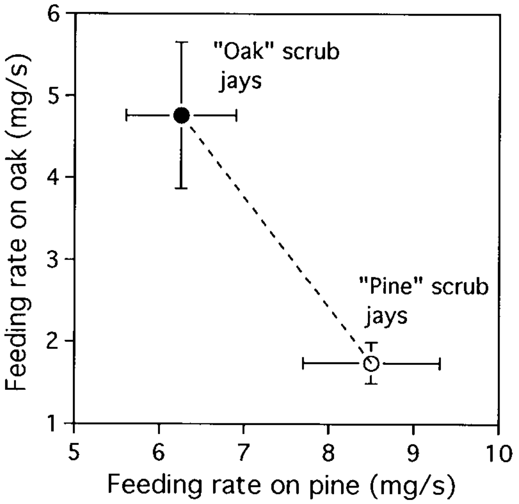

FIG. 4. Trade-off in feeding rates (mean ±1 SE) on pine cones and acorns. Feeding rates on pine were converted from seeds/s to mg/s by multiplying the mean feeding rate by the mean kernel mass of a pinyon (*P. monophylla*) seed (342.1 mg) (Vander Wall 1988). Pine and oak scrub-jays are represented by filled and empty circles, respectively.

about twice that for husking time on small gaps, as calculated from data in Table 3), making it more difficult to detect a significant difference.

One alternate explanation for the observed trade-off in feeding performance is that foraging on pine cones and acorns is a learned behavior, and is not related to differences in bill structure. Clearly, feeding performance does improve with experience to some extent. For example, the juvenile oak scrub-jay, which was undergoing its first season with acorns, had difficulty penetrating acorns in captivity. To minimize the possible effect of learning, we allowed the pine and oak scrub-jays a week or more to forage on acorns and pine cones, respectively, before we recorded data. If differences in experience continued to contribute to the differences in feeding performance between the two groups of adult scrub-jays, then over time, we should have detected increases in feeding performance on the alternative foods. However, over the course of the feeding trials we found no overall trend in improvement of feeding performance. Because the skills used in foraging on seeds are similar in kind if not magnitude, whether the seeds are pinyon or acorn, we suspect that improvements from learning occurred mostly early on, before we recorded data. For these reasons, we conclude that some if not most of the differences measured in adult feeding performance are attributable to differences in bill structure.

Our finding that oak scrub-jays were more efficient at husking relatively large and hard acorns than were pine scrub-jays was expected, because previous studies of seed-eating birds have consistently found that deeper billed birds husk large seeds more quickly than do shallower billed birds (Schluter 1982, Pulliam 1985, Benkman 1987, 1993, Price 1987, Smith 1987, Benkman and Pulliam 1988). Furthermore, it is easy to envision why large-billed birds, which can exert greater forces, can husk large and hard-shelled seeds faster than can small-billed birds. However it was more surprising to find that pine scrub-jays husked pinyon seeds substantially faster than did oak scrub-jays, because small-billed birds do not always husk small seeds faster than do large-billed birds. For example, some studies have found that small-billed birds husk small seeds faster than large-billed birds (e.g., Benkman 1987, 1993, Smith 1987, Benkman and Pulliam 1988), whereas other studies have shown that small- and large-billed birds husk small seeds at similar rates (e.g., Schluter 1982, Pulliam 1985). In addition, we are less certain which bill traits should be correlated with husking time on the thin-shelled pinyon seeds, especially since the larger billed Clark's Nutcracker, *Nucifraga columbiana* (Vander Wall and Balda 1981) husks pinyon seeds even faster than do the pine scrub-jays (see Vander Wall 1988). Although we are uncertain why pine scrub-jays husk pinyon seeds faster than do oak scrub-jays, the data support a strong trade-off in seed husking rates for pine and oak scrub-jays.

Correlations between bill characters and feeding performance

Further evidence of an adaptive basis for geographic variation in bill structure is the presence of consistent correlations between measures of bill size and shape, and measures of feeding performance. As predicted, feeding rates on pine cones were significantly higher for jays with relatively long and shallow bills (Table 5). Moreover, the positive correlations between bill length and shape, and feeding rates suggests our data (Table 3) may underestimate the relative differences in feeding rates on pine cones between the two subspecies of scrub-jays. The two groups of scrub-jays we used did not differ in bill length. However, with a much larger sample, Pitelka (1951) found a substantial difference in bill length and an even greater difference in bill shape than we found (Table 1). Consequently, if the birds we used had differed in bill length and shape to the extent that Pitelka found, we might have found an even greater difference in feeding rates on pine cones between the two scrub-jay populations.

Contrary to our expectation, hook length was not related to extraction time (Table 5). If hook length is not maladaptive for foraging on pine cones, then average hook length should not differ between populations, as suggested by Peterson (1993). Unfortunately, our data are inconclusive on this point. A plausible explanation for the lack of relationship between hook length and extraction time lies in the experimental setup. The location of perches next to the cone allowed scrub-jays to insert their bills into the scale gaps at almost any angle. This would have enabled scrub-jays to orient their bill hook along the widest axis of the gap, which was often perpendicular to the measured scale gap. Yet in the wild, scrub-jays often hover by cones to extract seeds (Vander Wall and Balda 1981), or at least have more limited perch sites. As a result, a long hook would more likely interfere with seed extraction. Thus, our experimental design may underestimate the impedance of a long hook during seed extraction.

We predicted that increases in bill stoutness and depth would decrease penetration time, whereas increases in bill stoutness and depth, curvature of culmen, and hook length would increase kernel removal rates on acorns. Increases in all four bill characters should also result in higher feeding rates. In general, these predictions held true, particularly when feeding on small acorns (Table 7). Failure to detect significant correlations in all of these relationships may have been a result of our small sample size.

In summary, the geographic variation in bill structure between scrub-jay populations occupying pinyon pine and oak woodlands is adaptive. The relatively long, shallow bill of the pine scrub-jay is adaptive for foraging on pine cones, and the deep, relatively stout, decurved, and hooked bill of the oak scrub-jay is adaptive for foraging on acorns. These conclusions are supported by the steep trade-off in feeding performance for pine and oak scrub-jays foraging on pine cones and acorns, and the moderate and often significant correlations between different measures of the bill structure and feeding performance. Bill shape as measured by bill length/depth is the metric related to the relative amount of pine and oak in the habitats of 12 different populations of scrub-jays (Fig. 3). Bill shape is also the metric that best accounted for the variation in feeding rates on pine cones and acorns.

Why aren't there two specialist scrub-jays in pine–oak woodland?

Scrub-jays have bill shapes that are intermediate between pine and oak specialists in woodland containing a mix of pinyon pine and oak (Fig. 3, Peterson 1993). Why a generalist scrub-jay is favored rather than a polymorphic scrub-jay composed of pine and oak specialists is unknown. One hypothesis is that neither resource alone in a pine–oak woodland is reliable enough to support specialists. Unfortunately, we do not have data to either support or reject this hypothesis. Another non-mutually exclusive hypothesis is that a population of generalists would outcompete a polymorphic population of two specialists in pine–oak woodland. Fitness set analysis (Levins 1968) can be used to test this hypothesis. If we assume that feeding rates can be equated to fitness then we can use Fig. 4 as a guide. A generalist would be favored in a pine–oak woodland if its combined feeding rates lie above and to the right of the dashed line connecting the feeding rates of the pine and oak scrub-jays (i.e., a convex fitness set). A generalist is favored because above and to the right of the dashed line the mean feeding rate or fitness of a generalist in the pine–oak woodland would be greater than the mean of the two specialists. Two specialists would be favored if a generalist's combined feeding rates lie below and to the left of the dashed line (i.e., a concave fitness set).

Ideally, we would have measured the feeding rates of scrub-jays from a pine–oak woodland to compare to the pine and oak scrub-jays. In the absence of such data, we divided the 10 scrub-jays into three groups based on bill shape, to create two specialist populations and one intermediate population (not shown). The feeding rates of the intermediate scrub-jays occurred above and to the right of the dashed line connecting the specialists. Although tentative because of the small sample sizes (only one and two individuals in the two specialist populations), it shows a convex fitness set where a population of generalist scrub-jays would outcompete a polymorphic population of two specialists in pine–oak woodland. This result, as well as the others, is consistent with the patterns of geographic variation in scrub-jays.

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LITERATURE CITED

Arnold, S. J. 1983. Morphology, performance and fitness. American Zoologist **23**:347–361.

Balda, R. P., and A. C. Kamil. 1989. A comparative study of cache recovery by three corvid species. Animal Behaviour **38**:486–495.

Beal, F. E. L. 1910. Birds of California in relation to the fruit industry. Part II. United States Department of Agriculture Biological Survey Bulletin **34**.

Benkman, C. W. 1987. Crossbill foraging behavior, bill structure, and patterns of food profitability. Wilson Bulletin **99**: 351–368.

Benkman, C. W. 1993. Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. Ecological Monographs **63**:305–325.

Benkman, C. W., and R. E. Miller. 1996. Morphological evolution in response to fluctuating selection. Evolution **50**: 2499–2504.

Benkman, C. W., and H. R. Pulliam. 1988. The comparative feeding rates of North American sparrows and finches. Ecology **69**:1195–1199.

Bent, A. C. 1946. Life histories of North American jays, crows, and titmice. Smithsonian Institute United States National Museum Bulletin **191**.

Boag, P. T., and A. van Noordwijk. 1987. Quantitative genetics. Pages 45–78 *in* F. Cooke and P. A. Buckley, editors.

Avian genetics: a population and ecological approach. Academic Press, New York, New York, USA.

Bowman, R. I. 1961. Morphological differentiation and adaptation in Galápagos finches. University California Publications in Zoology **58**:1–302.

Carmen, W. J. 1988. Behavioral ecology of the California scrub-jay (*Aphelocoma coerulescens californica*): a non-cooperative breeder with close cooperative relatives. Dissertation. University of California, Berkeley, California, USA.

Darwin, C. R. 1859. The origin of species by means of natural selection. John Murray, London, UK.

Davis, J. 1954. Seasonal changes in bill length of certain passerine birds. Condor **56**:142–149.

Gosler, A. G. 1987. Pattern and process in the bill morphology of the Great Tit, *Parus major*. Ibis **129**:451–476.

Grant, P. R. 1986. Ecology and evolution of Darwin's finches. Princeton University Press, Princeton, New Jersey, USA.

Grant, B. R., and P. R. Grant. 1989. Evolutionary dynamics of a natural population. University of Chicago Press, Chicago, Illinois, USA.

James, F. C. 1983. Environmental component of morphological differentiation in birds. Science **221**:184–186.

Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. Auk **104**:116–121.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, New Jersey, USA.

Mayr, E. 1963. Animal species and evolution. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.

Meyer, A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. Evolution **41**: 1357–1369.

Peterson, A. T. 1990. Evolutionary relationships of the *Aphelocoma* jays. Dissertation. University of Chicago, Chicago, Illinois, USA.

Peterson, A. T. 1991. Gene flow in scrub-jays: frequency and direction of movement. Condor **93**:926–934.

Peterson, A. T. 1993. Adaptive geographical variation in bill shape of Scrub-Jays (*Aphelocoma coerulescens*). American Naturalist **142**:508–527.

Peterson, A. T., and N. Vargas B. 1993. Ecological diversity in scrub-jays (*Aphelocoma coerulescens*). Pages 309–317 *in* T. P. Ramamoorthy, A. Lot, R. Bye, and J. Fa, editors. The biological diversity of Mexico: origins and distribution. Oxford University Press, Oxford, UK.

Pitelka, F. A. 1951. Speciation and ecologic distribution in American jays of the genus *Aphelocoma*. University California Publications in Zoology **51**:195–463.

Price, T. 1987. Diet variation in a population of Darwin's finches. Ecology **68**:1015–1028.

Pulliam, H. R. 1985. Foraging efficiency, resource partitioning, and the coexistence of sparrow species. Ecology **66**: 1829–1836.

Pyle, P. 1997. Identification guide to North American birds, Part I. Slate Creek Press, Bolinas, California, USA.

Ritter, L. V. 1983. Nesting ecology of scrub-jays in Chico, California. Western Birds **14**:147–158.

Schluter, D. 1982. Seed and patch selection by Galápagos ground finches: relation to foraging efficiency and food supply. Ecology **63**:1106–1120.

Smith, T. B. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. Nature **329**:717–719.

Sudworth, G. B. 1967. Forest trees of the Pacific slope. Dover, New York, New York, USA.

Vander Wall, S. B. 1988. Foraging of Clark's Nutcrackers on rapidly changing pine seed resources. Condor **90**:621–631.

Vander Wall, S. B., and R. P. Balda. 1981. Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. Zeitschrift für Tierpsychologie **56**:217–242.

Zusi, R. L. 1987. A feeding adaptation of the jaw articulation in New World jays (Corvidae). Auk **104**:665–680.