2006

Morphological variation in Clark's nutcracker (*Nucifraga columbiana*)

Karen Viotto
San Jose State University

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DOI: <https://doi.org/10.31979/etd.wu89-cgr6>
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MORPHOLOGICAL VARIATION IN CLARK'S NUTCRACKER
(*Nucifraga columbiana*)

A Thesis

Presented to

The Faculty of the Department of Biological Science

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Karen Viotto

December 2006

UMI Number: 1441131

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APPROVED FOR THE DEPARTMENT OF BIOLOGICAL SCIENCE

Dr. John O. Matson

Dr. Leslee Parr

Dr. Susan Lambrecht

APPROVED FOR THE UNIVERSITY

12/05/06

ABSTRACT

MORPHOLOGICAL VARIATION IN CLARK'S NUTCRACKER (*Nucifraga columbiana*)

By Karen Viotto

Morphological variation within a sample of Clark's Nutcracker (*Nucifraga columbiana*) from a museum collection was assessed for the contribution of age (three classes), sex, and locality. Mass, tail length, and six bill measurements were recorded for each specimen and potential sources of variation were assessed using univariate and multivariate analyses. Variation within this sample is relatively low. Variation due to age was evident in most characteristics examined and variation was highest among age class I (juveniles). *N. columbiana* males were larger in all eight measurements, with weight being the most dimorphic character. Variation between two geographically close samples was detected for three of the six bill measurements.

ACKNOWLEDGEMENTS

I am very grateful to John O. Matson for his advice, guidance, and assistance throughout this study, to Leslee Parr and Susan Lambrecht for their help in editing the manuscript and providing support and assistance. I thank San Jose State University for allowing me to work with the Nutcracker collection in the Bird and Mammal Museum and to L. Richard Mewalt for the collection of the specimens. I would like to thank Jenna Patton for her assistance with the data collection, Shannon Bros for help with the statistics, and Jean Geary for help with the specimens. I am particularly grateful to my husband, Dan Viotto, for believing in me, providing much support and encouragement, and showing great patience throughout this entire process.

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INTRODUCTION

Patterns of variation within and between populations are central to the development of our present understanding of evolutionary processes, specifically natural selection (Gould and Johnson 1972). Selection operates on variation among individuals in a population, thus variation in trophic-related characters (e.g., bill dimensions) and general characters (e.g., body size) must have been important in the evolution of birds. Valid comparisons within and across populations taking into account the relative importance of factors such as age and sex are needed to assess geographic variation.

Clark's Nutcracker (*Nucifraga columbiana*) is a member of the Family Corvidae, a large family among the Passeriformes composed of the familiar crows and jays, plus close relatives like magpies, treepies, and choughs. Corvids are social birds with sophisticated intelligence possessing cognitive tools such as causal reasoning, flexibility, imagination, and prospection (Emery and Clayton 2004). Evidence of these superior abilities can be seen in the specialized seed harvesting and caching abilities of several corvids, particularly the Clark's Nutcracker, whose behavioral techniques and bill morphology promote efficient exploitation of seed crops. These highly skilled birds are able to store large caches of seeds, which they can rely on to feed their young. Distinctive characteristics of the Clark's Nutcracker include a long sharp bill used to open conifer cones, extract seeds, and place seeds in caches (Vander Wall and Balda 1981); a sublingual pouch in which to transport large quantities of seeds (Bock *et al.*

1973); and an incubation patch in the male as well as the female (Mewalt 1952), allowing the male to incubate eggs while the female retrieves seeds from her caches.

Clark's Nutcrackers inhabit the high mountain regions of western North America. They are found from southern Alaska and southwestern Canada to Arizona and New Mexico, and northern Baja California, Sonora, and Nuevo León, Mexico (Bent 1964; Contreras-Balderas 1992; Howell and Webb 1995). The morphology, behavior, and annual cycle of the nutcracker is closely tied to their specialized diet of fresh and stored pine seeds, which has also influenced the ecology and evolution of several pines such as whitebark (*Pinus albicaulis*), limber (*P. flexilis*), Colorado piñon (*P. edulis*), single-leaf piñon (*P. monophylla*), and southwestern white (*P. strobiformis*) (Tomback 1998). Nutcrackers do not undergo latitudinal migration; however, they exhibit seasonal altitudinal movements in response to cone crops (Tomback 1998). Periodic irruptions, or shifts from their typical wintering grounds into other areas, sometimes occur in response to low seed availability. These extralimital occurrences sometime result in wide wanderings (as far as 1,800 km) of large numbers of nutcrackers moving away from their resident range (Fisher and Myres 1980).

The purpose of this study is to provide a quantitative examination of several morphological traits in a large sample of Clark's Nutcrackers. Analyses of morphometric data on sexed nutcrackers using a variety of statistical techniques is lacking and is needed in order to understand intrapopulation and interpopulation variability within this species. The specimens used in this study were part of a collection taken by L. Richard Mewalt while he was a graduate student affiliated with the Department of Zoology of Montana

State University (Mewalt 1948). Although Mewalt (1958) reported the means of some morphological measurements in his study on pterylography (the arrangement of feather tracts) and molt in Clark's Nutcrackers, he did not include a thorough analysis of morphological variation within the sample and between locations, sexes, and ages. The relative importance of each of these factors is assessed in this study and interpopulation variation between two geographically close samples is examined. Since no subspecies of Clark's Nutcrackers are recognized (Tomback 1998), implying little or no interpopulation variation; and, there are periodic movements away from their normal breeding grounds (Fisher and Myres 1980); and, it has a relatively narrow feeding niche (it is a food specialist) (Giuntoli 1963); then, this species should exhibit relatively little morphological variation according to the niche variation hypothesis (Van Valen 1965; Van Valen and Grant 1970).

MATERIALS AND METHODS

Sample

The specimens of *N. columbiana* used in this study were taken by L. R. Mewaldt from October, 1946, through October, 1951. A total of 439 specimens were collected. Of these, 428 were collected in western Montana, seven in eastern Washington, two in northern Idaho, and two in Oregon. The majority of birds collected in Montana were from two counties, Ravalli and Missoula. Although most collections were made in the winter and spring months, some specimens were taken in every month of the year (Mewalt 1958). These specimens are housed in the Bird and Mammal Museum at San Jose State University. Two hundred of these specimens were prepared as conventional study skins while the remaining were washed in detergent, slit open, and dried flat (Mewalt 1958). Only the flattened specimens were examined in this study because the upper and lower mandibles were completely separated from each other, thus allowing me to accurately measure and analyze each mandible independently. The sample sizes for each characteristic may vary because some bills were partially damaged or because data was not recorded on the specimen tag.

Age Classes

Age classes were determined by Mewalt (1948) on the basis of plumage characteristics, color descriptions, and gonadal development, as follows: Age class I

(Juveniles), include young birds that have acquired the power of sustained flight, but have not yet completed their partial post-juvenal molt. The body and head feathers are light mouse gray, frequently tipped with pale ochraceous-buff. Unlike yearlings and adults, there is an absence of white on the forehead and chin. Age class II (Yearlings), include individuals that have completed their post-juvenile molt, but can still be distinguished from adults. Age class III (Adults), are individuals that show no juvenile remiges, rectrices, bastard wing feathers, or wing coverts, usually by July of their second year of life.

Measurements

Two measurements were recorded from information on the specimen tags, tail length in centimeters and mass in grams. Bill measurements were taken to the nearest 0.05 mm using electronic digital, needle point calipers. Because skins had been split open and dried flat (Mewaldt 1958), the upper and lower mandibles were separated at the commissural point. This provided an ideal location to accurately measure upper and lower mandibles separately. Six bill characteristics were measured as described by Baldwin *et al.* (1931). These measurements were: upper mandible length, or the total culmen measurement, measured from the bill tip to the notch on the forehead where the base of the culmen meets the skull (just inside the feathers on the forehead); lower bill length, measured at the right commissural point to the tip of the lower bill; upper mandible depth, measured from the base of the exposed culmen at the edge of the

feathering to the cutting edge of the upper mandible, where the measurement is greatest; lower mandible depth, measured at the anterior margin of the chin to the cutting edge of the lower mandible, where the measurement is greatest; upper mandible width, measured at the base of exposed culmen of the upper mandible nearest the commissure; and, lower mandible width, measured at the base of exposed culmen of the lower mandible nearest the commissure.

Statistical Analyses

Univariate and multivariate statistical techniques were used to quantify the variation in this sample of *N. columbiana*. Computations were performed in the statistical packages Systat (v. 10) or SPSS (v. 11.5). As described by Straney (1978) and Leamy (1983), the contribution of sex, age, sex/age interaction, and error to the overall variation for each characteristic was assessed by use of a two-way ANOVA that partitioned the sums of squares for each factor (Norusis 1988). This procedure was performed twice, once with Ravalli County and once with Missoula County. Further differences between adult male and female Clark's Nutcrackers were examined with a *t*-test for each character.

Principal components analysis (PCA) was performed on adult Clark's Nutcrackers to describe the extent of individual variation in this sample. Data for this procedure were pooled from the entire collection of adults, which included 176 from western Montana, two from eastern Washington, and one from northern Idaho.

Interpopulation variation was assessed using a multiple analysis of variance

(MANOVA), which tested for differences in the means of the eight morphological traits between the two localities of Ravalli and Missoula County.

RESULTS AND DISCUSSION

Age Variation

Since the sample size for juveniles and yearlings from Ravalli County was quite small (juvenile males, $n = 5$; juvenile females, $n = 2$; yearling males, $n = 10$; yearling females, $n = 4$) investigation of age variation will be limited to the sample from Missoula County where samples were larger (juvenile males, $n = 9$; juvenile females, $n = 5$; yearling males, $n = 20$; yearling females, $n = 17$). Within this sample of *N. columbiana*, significant age variation was evident in all characteristics examined (Table 1). An average of 34% (range 12% to 70%) of the variation was due to age. Bill lengths contributed most to this variation (62% to 70%) and examination of the means show that bill lengths are distinctly smaller within age class I compared to the older age classes (Table 2). An explanation for this may be that these younger juvenile birds are just beginning to extract and cache seeds for themselves. Bill length is the primary trait needed for food manipulation in birds (Price *et al.* 1984), especially with nutcrackers who use their long bills to extract seeds from pine cones and to push seeds into the ground for caching. Helpless, altricial nutcrackers are fed by their parents and do not forage for themselves (Giuntoli 1963); therefore, a long bill would not be beneficial until the birds are capable of collecting their own food, which begins during the juvenile stage when nutcrackers acquire the power of sustained flight.

Also, the coefficients of variations for all characteristics (except lower bill depth in males) were highest among age class I (Table 2). Higher CV values within this age

class indicate that morphological change is greatest during the juvenile age compared to the yearling and adult stages.

Sexual Dimorphism

Results of variance partitioning indicate that the sample of *N. columbiana* from Missoula County had significant contributions to its variation due to the effect of gender for all eight measurements (Table 1). An average of over 9% (range 3% to 32%) of the variation in Missoula County was due to sex. The sample from Ravalli County had an average of 15% (range 0.4% to 34%) gender variation with five instead of eight variables showing significant sex contribution.

Patterns of gender variation differed between the two counties. *T*-tests revealed that samples from Ravalli County showed significant differences between the sexes for five characteristics (upper bill length, lower bill length, lower bill depth, tail length, and mass) while samples from Missoula County had differences for six characteristics (lower bill length, lower bill depth, upper bill width, lower bill width, tail length, and mass) (Table 3). Measurements from both locations were larger in males for all eight characteristics and the average difference between the sexes was 4.3% with the greatest difference being mass, which was 8.3% greater in males (Table 3). Mewalt (1958) also reported significant differences between adult male and female Clark's Nutcrackers in the portion of his collection not used in the present study (see Materials and Methods). Mewalt's measurements, along with the percent difference between the sexes, included wing length (3.1%), tail length (3.5%), exposed culmen length (6.0%), and bill height at

the angle of the gonys (4.5%), with all measurements being larger in males. Mewalt also reported no sexual differences in plumage or time and sequence of molt.

The degree of sexual dimorphism reported in this study and by Mewalt (1958) is fairly consistent with that recorded for another corvid, the Alpine Chough (*Pyrrhocorax graculus*). Delestrade (2001) found, on average, that Alpine Chough males are larger (from 4.5% to 13%) than females in all measurements, and as in the present study, the greatest difference between males and females was in weight. The second greatest difference between male and female nutcrackers, and Alpine Coughs (Delestrade 2001), was bill length. Since bill length is a primary feature associated with changes in requirements for food manipulation in birds (Price *et al.* 1984; Grant 1999), this may suggest that there are some differences in the feeding habits of male and female corvids. Giuntoli (1963) examined the food habits of Clark's Nutcrackers, but did not investigate differences between the sexes.

The prevailing explanation for larger-sized males is that those males are assumed to gain more mates through a selective advantage in terms of male-male competition or female choice (Darwin 1871). Competition may arise when there are more males than females, resulting in several males not obtaining mates. The sex ratio of Clark's Nutcrackers is difficult to determine; however, among 439 specimens collected by Mewaldt (1958), the juvenile sex ratio was equal, but adult males outnumbered females 2:1. Whether this reflects sampling bias or differences in mortality needs to be studied.

Individual Variation

The extent of individual variation is indicated by the coefficient of variation (CV). The CV's of the eight morphological measurements for adult males and females from Missoula ranged from 2.4% to 8.5% (Table 2). When data were pooled for all adults from both locations, upper bill depth was the most variable measurement (CV = 7.7%) followed by mass (CV = 7.5%), lower bill width (CV = 5.9%), upper bill length (CV = 5.7%), lower bill length (CV = 5.5%), upper bill width (CV = 4.4%), lower bill depth (CV = 4.2%), and tail length (CV = 3.7%). Adult females displayed greater variability in all characteristics excluding tail length. It is possible that the weight of females varied more than males because samples were collected throughout the year and may have included females in varying states of reproduction.

The only data available with which to compare morphological variability in corvids is from Delestrade (2001), who reported similar results in the Alpine Cough with CV values varying from 2.2% to 8.5% for weight, bill dimensions, wing length, tarsus length, and tail length. The most variable trait in the Alpine Coughs was weight followed by bill depth. Wiens and Rotenberry (1980) reported the CV's for a number of bill and body measurements in eleven species within the order Passeriformes and one within the order Charadriiformes (CV = 2 - 8%). They found the average CV's for bill width and body mass to be significantly greater than those of the other characters. Radford and Du Plessis (2004) reported CV's of 2.3% to 5.9% for bill and body measurements in a population of Green Woodhoopoes (*Phoeniculus purpureus*), belonging to the order

Coraciiformes. The individual variation found in the present study appears to be a common trend in several bird species.

The first five eigenvalues from the principle components analysis (PCA) were needed to account for 91.2% of the total variation (Table 4), indicating that the morphological variation in this sample is relatively low. The first eigenvalue (corresponding to principal component I) accounts for 35.9% of the variation and the variable loadings are all positive. PC I is characterized most by bill lengths (0.74), which demonstrates the importance of these traits in an avian species that relies on a long bill to extract seeds from cones and to push the seeds into the ground for caching.

The second eigenvalue (corresponding to PCII) accounts for 17.4% of the variation in the data sample (Table 4). Although PCII accounts for little variation, the most influential variables are upper bill depth and bill widths and loadings for these characteristics are negative. These negative loadings may suggest a slightly opposing correlation between depth and width in relation to bill length.

Interpopulation Variation

The analyses of sexual dimorphism reported in this study revealed different patterns of variation between Ravalli and Missoula County; therefore, further analysis of interpopulation variation was assessed using a multiple analysis of variance (MANOVA) to test for the main effects of location and sex on the combination of the eight morphological response variables. No significance was found for the interaction of location and sex (Table 5). This finding indicates that the proportions of the

measurements of these morphological traits do not differ among the males and females between the two counties; however, significant differences were found between the two locations (Wilk's Lambda = 0.815, $P < 0.001$). Lower bill width, upper bill length, and upper bill depth contributed significantly to this group difference. Since bite force in birds correlates strongly with bill depth and width (Herrel *et al.* 2004), and the range of seed sizes collected correlates most with bill depth (Diaz 1994), and bill length is associated with changes in requirements for food manipulation (Price *et al.* 1984; Grant 1999), this variation in bill morphology between these two groups of nutcrackers may suggest some variability in food supply between the two locations.

Contreras-Balderas (1992) reported tail size of a specimen from a relict population from Nuevo León, Mexico, as substantially longer (123.3 mm) than the range of 111.0-118.5 (n = 6) given by Ridgeway (1904). Tail lengths in this present study, measured by Mewalt (1958), range from 103.2-123.7 mm. The tail of the specimen from the relict population falls within this range; thus, it cannot be considered substantially longer than tails of nutcrackers found north of Mexico.

In order to fully describe geographic variation in nutcrackers, morphometric data on more distant populations are needed. However, I suspect that geographic variation will not be very prominent in Clark's Nutcrackers. First of all, no subspecies of Clark's Nutcrackers have been identified, indicating a relatively homogenous species throughout its range. Second, the home range of nutcrackers is relatively large for a passerine (Tomback 1998) and they emigrate outside their normal breeding range in response to low food availability (Giuntoli 1963; Vander Wall *et al.* 1981). This movement would

allow more opportunities for gene flow between populations. Third, Clark's Nutcrackers are food specialists, and according to the niche variation hypothesis (Van Valen 1965; Van Valen and Grant 1970), should be less variable morphologically than those which have generalized food habits. In contrast, the scrub-jay (*Aphelocoma coerulescens*), a close relative of the Clark's Nutcracker, exhibits pronounced adaptive geographic variation in a number of characters, especially in the size and shape of the bill (Bardwell *et al.* 2001; Peterson 1993). Unlike Clark's Nutcrackers, several subspecies of scrub-jays have been recognized, they are non-migratory, and adults are territorial year round (Ritter 1983; Carmen 1988).

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TABLE 1. Results of variance partitioning of *N. columbiana* using the two-way ANOVA for all age classes (1-3) for Missoula County and Ravalli County.

Measurement	Ravalli County				Missoula County			
	Age	Sex	Sex/Age	Error	Age	Sex	Sex/Age	Error
Upper bill length	0.90	33.61**	4.10	61.39	62.23**	3.13**	0.12	34.52
Lower bill length	0.07	19.17**	1.45	79.31	69.94**	6.39**	0.15	23.51
Upper bill depth	2.09	1.09	0.40	96.42	22.43**	3.07*	1.53	72.96
Lower bill depth	6.43*	21.20**	0.27	72.11	31.85**	10.32**	1.68	56.16
Upper bill width	0.60	0.42	0.86	98.12	23.94**	3.68*	3.06	69.32
Lower bill width	2.35	2.36	5.21	90.09	20.92**	6.77**	3.60	68.71
Tail length	33.08**	14.97**	0.34	51.61	28.36**	9.73**	6.20**	55.71
Mass	0.14	30.94**	0.04	68.88	11.98**	32.19**	3.20*	52.63

* P < 0.05

**P < 0.01

TABLE 2. Descriptive statistics for eight external measurements in three age classes of male and female Clark's Nutcrackers (*N. columbiana*) from Missoula County.

Measurements	Age	Males					Females				
		n	Mean	Range	SD	CV	n	Mean	Range	SD	CV
Upper bill length	Juvenile	10	29.40	24.9-33.0	2.50	8.51	5	27.66	23.2-32.3	4.41	15.93
	Yearling	21	37.13	35.0-40.5	1.45	3.90	16	35.64	32.0-37.9	1.35	3.80
	Adult	41	37.75	32.2-42.0	2.09	5.54	23	36.68	31.1-42.3	2.35	6.40
Lower bill length	Juvenile	9	31.88	28.2-34.3	2.18	6.85	5	29.38	24.5-33.1	3.33	11.33
	Yearling	19	39.41	37.2-42.1	1.15	2.93	16	37.86	34.3-40.5	1.90	5.01
	Adult	40	41.23	36.5-44.4	1.62	3.94	23	39.27	35.1-44.0	1.98	5.04
Upper bill depth	Juvenile	10	8.73	6.5-9.9	1.22	14.00	5	8.07	6.6-9.1	1.02	12.68
	Yearling	21	9.58	8.6-10.4	0.38	4.00	17	9.53	8.6-10.1	0.35	3.64
	Adult	41	9.71	8.5-11.7	0.55	5.71	23	9.38	6.2-10.2	0.80	8.50
Lower bill depth	Juvenile	10	4.98	4.9-5.2	0.11	2.13	5	4.57	3.4-5.1	0.71	15.43

Measurements	Age	Males					Females				
		n	Mean	Range	SD	CV	n	Mean	Range	SD	CV
	Yearling	20	5.37	5.0-5.7	0.21	3.85	17	5.19	5.0-5.4	0.11	2.17
	Adult	41	5.41	5.0-5.8	0.19	3.46	22	5.25	4.9-5.8	0.23	4.40
Upper bill width	Juvenile	10	15.29	13.1-16.3	0.96	6.29	5	14.42	12.0-16.8	1.90	13.17
	Yearling	20	16.15	15.1-18.2	0.83	5.16	17	16.23	15.2-17.7	0.71	4.35
	Adult	41	16.59	15.4-17.6	0.59	3.56	23	16.06	15.0-17.6	0.71	4.42
Lower bill width	Juvenile	9	14.24	11.0-16.0	1.18	10.37	5	12.57	10.6-14.0	1.40	11.18
	Yearling	20	15.22	13.7-16.9	0.77	5.07	17	15.01	13.8-16.3	0.81	5.42
	Adult	41	15.45	14.0-17.6	0.79	5.14	23	14.84	12.2-16.3	1.07	7.21
Tail length	Juvenile	10	10.52	7.5-11.6	1.18	11.19	5	9.02	6.7-10.6	1.83	20.37
	Yearling	19	10.98	10.4-11.6	0.28	2.59	14	10.67	10.1-11.8	0.40	3.79
	Adult	30	11.39	10.8-12.4	0.35	3.04	19	11.02	10.6-11.5	0.26	2.40
Mass	Juvenile	10	134.33	116.2-147.5	9.60	7.15	5	109.64	103.2-125.6	9.14	8.34

Measurements	Age	Males					Females				
		n	Mean	Range	SD	CV	n	Mean	Range	SD	CV
	Yearling	21	142.33	132.1-153.2	5.15	3.62	17	130.56	119.4-140.5	6.30	4.83
	Adult	41	142.49	125.0-160.6	9.38	6.58	23	130.67	115.2-154.6	9.93	7.60

TABLE 3. Comparisons of adult male and female *N. columbiana* from Ravalli and Missoula Counties. Significant differences between the sexes are based on *t*-tests.

Measurement	Sex	Ravalli County				Missoula County			
		n	Mean	SD	P	n	Mean	SD	P
Upper bill length	Male	54	37.9	1.5		41	37.7	2.10	
	Female	22	35.0	1.7	0.000**	23	36.7	2.30	0.065
Lower bill length	Male	53	40.8	2.8		40	41.2	1.60	
	Female	21	38.3	1.7	0.000**	23	39.3	2.00	0.000**
Upper bill depth	Male	55	9.9	0.8		41	9.7	0.60	
	Female	22	9.7	0.8	0.280	23	9.4	0.80	0.057
Lower bill depth	Male	55	5.5	0.2		41	5.4	0.20	
	Female	21	5.2	0.1	0.000**	22	5.2	0.20	0.005**
Upper bill width	Male	55	16.5	0.8		41	16.6	0.60	
	Female	22	16.4	0.7	0.616	23	16.1	0.70	0.002**

Measurement	Sex	Ravalli County				Missoula County			
		n	Mean	SD	P	n	Mean	SD	P
Lower bill width	Male	55	15.8	0.7		41	15.5	0.80	
	Female	21	15.5	1.0	0.063	23	14.8	1.10	0.012*
	Male	49	11.4	0.4		30	11.4	0.30	
Tail length	Female	20	11.0	0.4	0.000**	19	11.0	0.30	0.000**
	Male	55	142.3	8.5		41	142.5	9.40	
Mass	Female	22	130.6	8.4	0.000**	23	130.7	10.00	0.000**

* P<0.05

**P<0.01

TABLE 4. Results of Principal Components Analysis for adult *N. columbiana* from central western Montana (n = 176), eastern Washington (n = 2), and northern Idaho (n = 1).

Component	Eigenvalues	Percent	PC Loadings	PC I	PC II
1	2.871	35.89	Upper length	0.736	0.463
2	1.3925	17.40	Lower length	0.744	0.247
3	0.9187	11.49	Upper depth	0.334	-0.676
4	0.7904	9.88	Lower depth	0.663	-0.076
5	0.6922	8.65	Upper width	0.464	-0.560
6	0.6307	7.89	Lower width	0.392	-0.512
7	0.4545	5.69	Tail length	0.638	0.272
8	0.2499	3.12	Mass	0.670	0.058

TABLE 5. MANOVA results testing the main effect of location and sex on the combination of the eight morphological response variables.

Effect	Wilks' Lambda	F-Statistic	df	P
Location/Sex	0.907	1.321	8	0.241
Location	0.815	2.927	8	0.006**
Sex	0.529	11.446	8	0.000**

Effects of location on each character.

Source	df	F	P
Upper bill length	1	6.156	0.015*
Lower bill length	1	1.414	0.237
Upper bill depth	1	6.144	0.015*
Lower bill depth	1	1.736	0.19
Upper bill width	1	1.39	0.241
Lower bill width	1	14.203	0.000**
Tail length	1	0.013	0.91
Mass	1	0.3	0.585

* P< 0.05

**P< 0.01