

PLUMAGE, SIZE, AND SEXUAL DIMORPHISM IN THE QUEEN CHARLOTTE ISLANDS HAIRY WOODPECKER¹

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Abstract. Plumage, size, and sexual dimorphism of the endemic Hairy Woodpecker subspecies *Picoides villosus picoideus* are described and compared with a less isolated insular population. Museum specimens of *P. v. picoideus* from the Queen Charlotte Islands, British Columbia were compared with *P. v. harrisi* specimens from Vancouver Island, British Columbia. Specimens from the two localities are similar in size, although the culmen of *P. v. picoideus* is 5–6% shorter. In plumage, *P. v. picoideus* is distinct in having markings on the belly and flanks, dorsal barring, and barring on the outer rectrices. The breast and belly are much darker and the wing coverts have fewer white markings in *P. v. picoideus* than in *P. v. harrisi*. Adults and juveniles, and adult males and females, differ only in minor features of plumage. Adult plumage of *P. v. picoideus* and insular populations of *P. villosus* in Newfoundland and the Grand Bahamas resembles juvenal plumage in mainland locations, and includes ancestral traits in this woodpecker lineage. Sexual dimorphism in size is similar in *P. v. picoideus*, *P. v. harrisi*, and continental populations, suggesting no ecological release of the sexes on the Queen Charlotte Islands or Vancouver Island. Relative sexual dimorphism in bill size varies little over the species' range, hence appears to be influenced little by ecological factors.

Key words: Hairy Woodpecker, island biology, Pacific Northwest, *Picoides villosus*, Queen Charlotte Islands, sexual dimorphism, Vancouver Island.

INTRODUCTION

The Hairy Woodpecker (*Picoides villosus*) is a permanent resident over a broad range, from tree line in Alaska and northern Canada south to Costa Rica and Panama. Over this range, the species inhabits diverse forested habitats from sea level to 4,000 m (Short 1982, Jackson and Ouellet 1999). Extensive geographic variation in plumage and size occurs (Ouellet 1977, Short 1982), hence many subspecies have been recognized (AOU 1957, Winkler et al. 1995, Pyle 1997). One broad pattern of variation is an increase in body size from south to north. Another is of drab underparts occurring in birds from southeastern Alaska, "west of the western foothills of the Rocky Mountains to western Texas, northern Baja California, and western Panama" (Ouellet 1977), and white underparts east of there (Coues 1877, Jenkins 1906). Strong patterns of differentiation also appear on smaller

spatial scales (Dehnel 1948). Differentiation between eastern and western forms may reflect postglacial colonization from and adaptation to the two great forested Pleistocene refugia in southwestern and southeastern North America (Voous 1947, Moore and Price 1993), although genetical evidence supporting this evolutionary scenario is wanting (Klicka and Zink 1997).

The distinctive subspecies *P. v. picoideus* is endemic to the Queen Charlotte Islands, British Columbia (Osgood 1901, Short 1982). It is one of several species of birds on the Queen Charlotte Islands that have differentiated relative to mainland forms (Aldrich 1968, Phillips 1991). Ecological factors responsible for avian differentiation on the archipelago have not been investigated, but feeding competition is one likely cause. In some insular populations of woodpeckers, ecological release from feeding competition has promoted sexual divergence in foraging behavior and size of the feeding apparatus (Selander 1966, 1972).

The main purpose of this study was to inves-

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tigate the possibility that ecological release led to enhanced sexual differences in size of *P. v. picoideus* on the Queen Charlotte Islands. Secondary aims were to describe body size and sexual differences in plumage, which are commonly affected by insularity.

In this paper we describe size and plumage of *P. v. picoideus*, with particular reference to sexual differences. We compare our findings with those from parallel analyses on the coastal subspecies *P. v. harrisi* from Vancouver Island, British Columbia. Vancouver Island was selected for comparison because it is roughly the same size as the Queen Charlotte Islands and because *P. v. harrisi* there is similar in body size to *P. v. picoideus*. In addition, more species of woodpecker inhabit Vancouver Island than the Queen Charlotte Islands (six vs. three; Godfrey 1986), and Vancouver Island has few or no barriers to gene flow with the mainland because of direct proximity and the presence of intervening islands. In contrast, the Queen Charlotte Islands are about 50 km south of Dall Island, Alaska, 50 km west of Porcher Island (adjacent to the British Columbia mainland), and 225 km north of Vancouver Island.

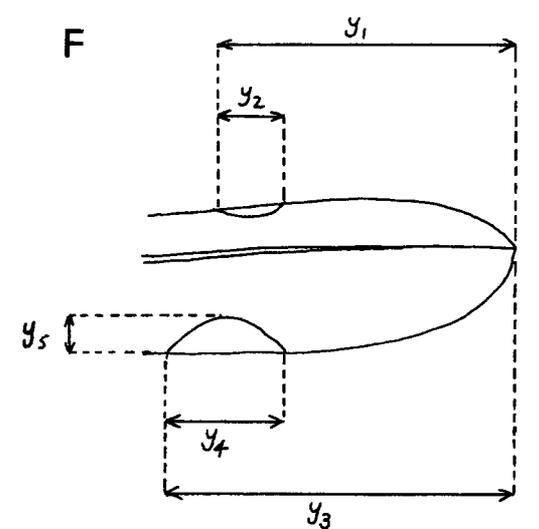
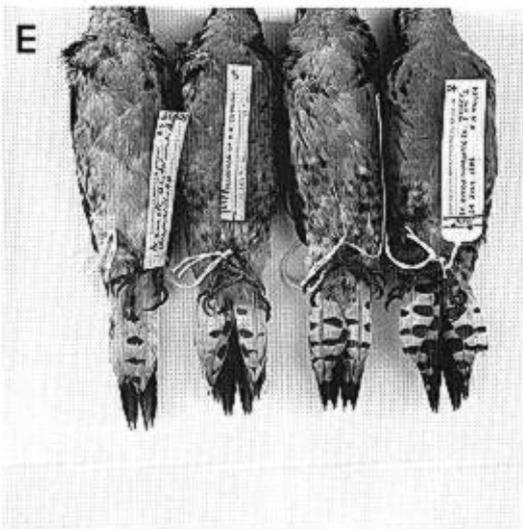
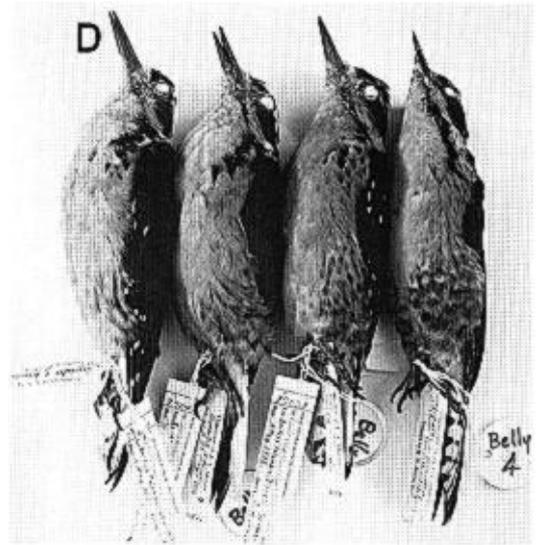
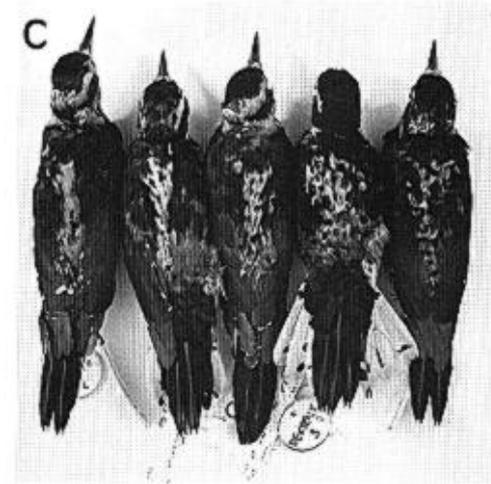
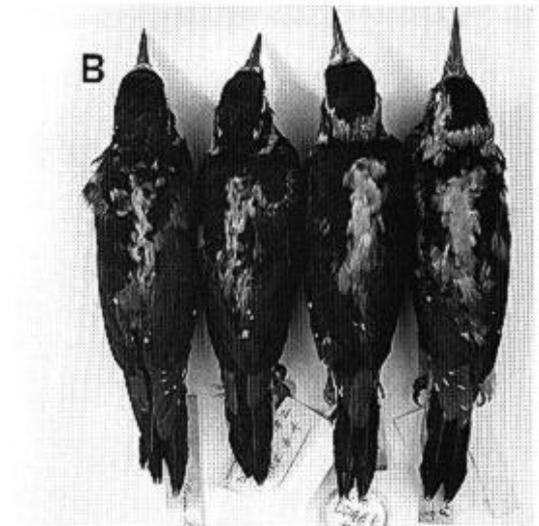
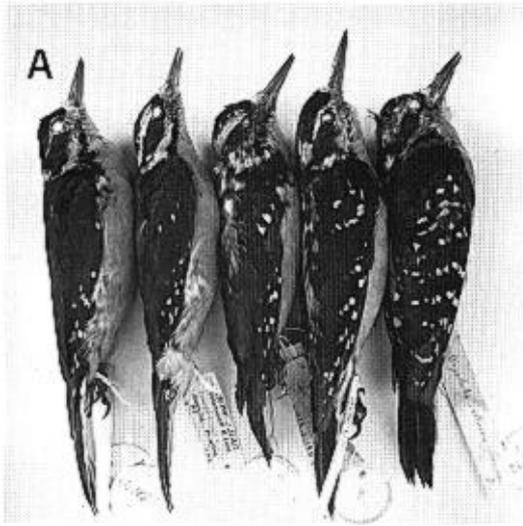
METHODS

This study is based upon an examination of 246 study skins from 18 museums (128 from the Queen Charlotte Islands [QCI], 118 from Vancouver Island [VI]): Academy of Natural Sciences; American Museum of Natural History; British Museum (Natural History; London, United Kingdom); Carnegie Museum; Cowan Museum (Vancouver, British Columbia, Canada); Field Museum; Forschungsinstitut Senckenberg (Frankfurt, Germany); Merseyside County Museums (Liverpool, United Kingdom); Museum of Vertebrate Zoology; National Museum of Natural History; National Museum of Natural Sciences (Ottawa, Ontario, Canada); Natural History Museum (Basel, Switzerland); Peabody Museum; Royal British Columbia Museum (Victoria, British Columbia, Canada); Royal Ontario Museum (Toronto, Ontario, Canada); University Museum (Oxford, United Kingdom); University of Illinois at Urbana-Champaign; University of Michigan; and University of Puget Sound. The seasonal distribution of specimens of known sex and with known collecting dates was (QCI females-QCI males-VI females-VI males): January (0-1-6-5), February (0-1-3-4),

March (1-1-6-5), April (4-7-6-5), May (15-17-10-12), June (13-26-3-6), July (9-7-2-8), August (4-7-4-2), September (1-4-1-4), October (0-2-4-3), November (1-0-3-2), and December (1-1-3-6).

The following variables were measured with digital calipers or ruler except as noted: length of flattened wing, to 1 mm; chord of exposed culmen, to 0.1 mm; chord from bill tip to anterior edge of nares, to 0.1 mm; tarsal length, to 0.1 mm; tail length, to 1 mm; chord of claw on digit IV, from tip of claw to dorsal junction of claw with toe, to 0.1 mm (measured with 8× dissecting microscope and ocular micrometer); and several variables on primary VIII, to 1 mm (Fig. 1F). Some seasonal variation in measurements occurs but shows no obvious trends (Jackson 1970), so specimens collected at different seasons were combined. The two measurements on bill length were highly correlated, so most analyses were conducted only on chord of exposed culmen.

Plumage attributes were scored against reference series for each variable (Fig. 1A-E). Separate reference series were established for the two geographic samples for purposes of characterizing sexual dimorphism in each locality. Reference series included juveniles, although these were excluded from most analyses (see Results). High repeatability was established by scoring specimens against the series before setting the ranges for final scoring. The final number of score categories ranged from three to five for different variables, and differed between geographic samples. Plumage variables were: darkness of breast and belly (1 = palest, 3 = darkest for QCI, 5 = darkest for VI); darkness of white plumage in median dorsal stripe (1 = palest, 4 = darkest); darkness of supercilium (1 = palest, 3 = darkest); darkness of moustachial stripe (1 = palest, 3 = darkest); extent of belly and flank markings (1 = least, 4 = most; QCI only); amount of black markings on white areas of the rectrices (1 = none [hypothetical only; none observed], 5 = greatest; QCI only); area of median dorsal stripe (1 = smallest, 4 = largest); amount of black markings in median dorsal stripe (1 = least, 5 = greatest); and amount of white markings in wing coverts (1 = none, 5 = greatest). As for measurements, seasonal changes in plumage are minor and unsystematic (Jackson 1970), although Ouellet (1977) noted increased whiteness from fall to spring in eastern



P. villosus. Seasonal differences were not found in this study.

First-year birds were distinguished using criteria of Osgood (1901), Jackson (1970), George (1972), and Short (1982). Ouellet (1977) suggested that darkness of underparts is unrelated to age, and Jackson (1970) commented on the similarity of first-winter and adult plumage in the species. However, Bent (1939) noted that "the white spots are not quite so pure white" (presumably referring to coverts) in first-year *P. v. villosus*. That observation, and slight differences noted in the present study, led us to exclude first-year specimens from most analyses.

DATA ANALYSIS

Simple linear regression was used where some predictive effect or cause of the independent variable seemed reasonable, such as sexual dimorphism in size relative to body size. Reduced major axis regression was used when both variables were measured with error and there was no presumed effect of one variable on another, such as male and female sizes within populations (Ricker 1973). Polynomial regression was used to describe the relationship of bill size to body size across geographic samples (data from Ouellet [1977] and this study). Following procedures in Sokal and Rohlf (1981), quadratic expressions were determined to be a better fit than higher-order polynomials or simple linear regressions for those data.

Sexually dimorphic structures often exhibit positive allometry with body size (Andersson 1994). To investigate this possibility, simple linear regression of the chord of exposed culmen on length of flattened wing was carried out for each sex in the QCI and VI samples.

Reduced major axis regression was fitted with Kaleidagraph 3.0 (Abelbeck Software, 2457 Perkiomen Avenue, Reading, PA 19606). Analysis of variance (one- and two-way ANOVAs and MANOVAs) was carried out with SuperAnova 1.11 (Abacus Concepts, 1918 Bonita Avenue, Berkeley, CA 94704). Simple linear regression,

polynomial regression, and other analyses were done with Statview 4.5 (Abacus Concepts). In regressions, residuals were examined for normality, homogeneity of variance, and independence.

RESULTS

DIFFERENCES BETWEEN GEOGRAPHIC SAMPLES

Hairy Woodpeckers were of similar size on QCI and VI, although some differences were found: QCI females had longer wings and males had longer tarsi than did VI specimens (Table 1). Length of exposed culmen differed strongly between the two areas, however, averaging about 3 mm shorter on QCI for both sexes (Table 1). Markings on primary VIII showed few differences between localities. In QCI adults, the proximal edge of the marking on the feather's posterior margin was closer to the feather tip than in VI specimens (variable P3; Table 1). In females, this marking was smaller in QCI than in VI specimens (variable P4; Table 1). Two-way ANOVAs confirmed those trends and disclosed a significant interaction term for variable P4: sexual differences within the two geographic samples were in opposite directions (Tables 1 and 2).

AGE VARIATION IN PLUMAGE

First-year and adult specimens differed slightly in characters of primary VIII (Table 1), and in body plumage: QCI adults had paler underparts (females) and a darker supercilium (males); VI adults of both sexes had less black in the median dorsal stripe (Table 3).

SEXUAL AND INDIVIDUAL VARIATION IN PLUMAGE

Minor sexual differences in plumage were noted. On primary VIII, the proximal edge of the marking on the feather's posterior margin was farther from the feather tip in VI females than in males (variable P3); this marking was larger in QCI males than females (variable P4), and in

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FIGURE 1. Examples of reference series of Hairy Woodpeckers for scoring plumage characteristics (A–E), and variables on primary VIII (F). A—amount of white markings on wing coverts (Vancouver Island; scores 1–5). B—area of median dorsal stripe (Vancouver Island; scores 1–4). C—amount of black markings in median dorsal stripe (Queen Charlotte Islands; scores 1–5). D—extent of belly and flank markings (Queen Charlotte Islands; scores 1–4). E—amount of black markings on white areas of the rectrices (Queen Charlotte Islands; scores 2–5). F—right primary VIII in dorsal view, showing five variables measured on it.

TABLE 1. Descriptive statistics for continuous variables (adult specimens only).^a

Variable	Queen Charlotte Islands ^b		Vancouver Island ^b	
	Female	Male	Female	Male
Body mass (g)	72.8 ± 3.1 (5)	80.1 ± 2.9 (4)	—	—
Length, flattened wing (mm)	127.1 ± 0.4 ^c (34)	128.7 ± 0.4 (52)	125.4 ± 0.4 ^c (45)	128.1 ± 0.4 (54)
Chord, exposed culmen (mm)	28.1 ± 0.2 ^d (33)	31.5 ± 0.2 ^c (52)	30.9 ± 0.2 ^d (43)	34.5 ± 0.2 ^c (54)
Chord, bill tip to anterior edge of nares (mm)	24.6 ± 0.2 (32)	27.7 ± 0.2 (50)	27.3 ± 0.2 (43)	30.4 ± 0.2 (54)
Tarsal length (mm)	21.7 ± 0.1 (34)	22.7 ± 0.1 ^f (53)	21.6 ± 0.1 (44)	22.1 ± 0.1 ^f (54)
Tail length (mm)	77.1 ± 0.8 (31)	76.3 ± 0.7 (46)	77.4 ± 0.6 (41)	77.9 ± 0.6 (47)
Chord, claw IV (mm)	6.48 ± 0.05 (34)	6.83 ± 0.03 (53)	6.57 ± 0.04 (45)	6.88 ± 0.04 (54)
P1 (mm)	35.4 ± 1.2 (34)	34.7 ± 1.4 ^g (53)	32.6 ± 1.3 ^h (45)	33.3 ± 1.3 (54)
P2 (mm)	2.47 ± 0.15 (34)	2.70 ± 0.20 (53)	2.58 ± 0.13 (45)	2.65 ± 0.15 (54)
P3 (mm)	45.5 ± 0.9 ⁱ (34)	43.9 ± 0.8 ^{jk} (51)	50.4 ± 0.8 ^{i,lm} (45)	47.2 ± 0.8 ^{i,m} (52)
P4 (mm)	3.24 ± 0.16 ^{n,o,p} (34)	3.75 ± 0.16 ^p (51)	3.96 ± 0.18 ⁿ (45)	3.67 ± 0.18 (52)
P5 (mm)	3.35 ± 0.21 (34)	3.18 ± 0.15 (51)	3.91 ± 0.21 ^q (45)	3.27 ± 0.20 ^q (52)

^a Cell entries are Mean ± SE (n). For explanation of P1–P5, see Figure 1.
^b Within localities, sexes differed significantly ($P < 0.05$) on all body measurements except tail length.
^c Females between localities: $P < 0.01$ (by one-way ANOVA, here and below).
^d Females and males between localities: $P < 0.001$.
^e Males between localities: $P < 0.01$.
^f Male adults vs. juveniles [juveniles = 29.3 ± 2.1 (20)]: $P < 0.05$.
^g Female adults vs. juveniles [juveniles = 22.1 ± 4.8 (7)]: $P < 0.01$.
^h Females and males between localities: females, $P < 0.001$; males, $P < 0.01$.
ⁱ Male adults vs. juveniles [juveniles = 40.4 ± 1.4 (20)]: $P < 0.05$.
^j Female adults vs. juveniles [juveniles = 42.9 ± 2.2 (7)]: $P < 0.01$.
^k Females vs. males: $P < 0.01$.
^l Females between localities: $P < 0.01$.
^m Female adults vs. juveniles [juveniles = 4.36 ± 0.44 (14)]: $P < 0.01$.
ⁿ Females vs. males: $P < 0.05$.

VI females than males (variable P5). QCI males had darker underparts than females, and VI males had a darker dorsal median stripe than females (Table 3).

TABLE 2. Summary of results from two-way ANOVAs on continuous variables, for variables that exhibited statistically significant differences.

Variable	Locality ^a	Sex	Interaction
	QCI vs. VI	Male vs. female	Sex × locality
Length, flattened wing	***	***	
Chord, exposed culmen	***	***	
Tarsal length	***	***	
Chord, claw IV		***	
P3	***	***	
P4			*
P5		*	

^a QCI = Queen Charlotte Islands; VI = Vancouver Island.
 * $P < 0.05$, *** $P < 0.001$.

SEXUAL VARIATION IN MEASUREMENTS

Data on measurements and sexual dimorphism are summarized in Tables 1, 3, and 4. Males were much larger than females in length of culmen (12%), moderately larger in chord of claw and in tarsal length (3–5%), and slightly larger in length of flattened wing (1–2%); tail length did not differ between the sexes. As noted above, QCI males had longer tarsi than VI males, which accounts for the greater sexual dimorphism in tarsal length in the QCI sample (= 4.4%, vs. 2.6% on Vancouver Island). As expected, MANOVAs disclosed highly significant sexual differences in size in each geographic sample ($P < 0.001$).

All regressions of length of exposed culmen on length of flattened wing were statistically nonsignificant ($P > 0.05$), indicating independence of the two traits within localities.

TABLE 3. Data summary for plumage scores.^a

Character scored	Queen Charlotte Islands		Vancouver Island	
	Female	Male	Female	Male
Darkness, breast and belly	1.42 ^{b,c} (1-3)	2.00 ^b (1-3)	2.47 (1-5)	2.93 (1-5)
Darkness, dorsal stripe	2.19 (1-4)	2.42 (1-4)	2.00 ^d (1-4)	2.22 ^d (1-4)
Darkness, supercilium	1.88 (1-3)	1.91 ^e (1-3)	1.80 (1-3)	1.81 (1-3)
Darkness, moustachial stripe	2.50 (2-3)	2.38 (1-3)	2.24 (1-3)	2.30 (1-3)
Extent, belly and flank markings	1.75 (1-4)	1.47 (1-4)	—	—
Amount, black rectrix markings	2.05 (1-5)	2.19 (1-5)	—	—
Area, dorsal stripe	2.50 (1-4)	2.10 (1-4)	2.73 (1-4)	2.52 (1-4)
Amount, black markings in dorsal stripe	3.33 (1-5)	3.14 (1-5)	0.89 ^f (1-3)	0.88 ^g (1-2)
Amount, white markings in wing coverts	2.20 (1-5)	2.30 (1-5)	2.68 (1-5)	2.81 (1-5)

^a Cell entries are median (range).
^b Females vs. males: $P < 0.01$ (by Chi-square test here and below, except as noted).
^c Female adults vs. juveniles (juvenile median = 2.21): $P = 0.02$ (Fisher's Exact Test, with score categories >1 combined).
^d Females vs. males: $P < 0.05$.
^e Male adults vs. juveniles (juvenile median = 1.67): $P = 0.01$ (Fisher's Exact Test, with score categories >1 combined).
^f Female adults vs. juveniles (juvenile median = 1.69): $P = 0.03$ (Fisher's Exact Test, with score categories >1 combined).
^g Male adults vs. juveniles (juvenile median = 1.75): $P = 0.02$ (Fisher's Exact Test, with score categories >1 combined).

DISCUSSION

In general features of plumage, Hairy Woodpeckers are darker on the Queen Charlotte Islands than elsewhere in their range, closely followed by those from Vancouver Island and the adjacent mainland (from southeastern Alaska to northern California; Swarth 1922, Ouellet 1977). We found that males of *P. v. piceoides* had darker underparts than females. Ouellet (1977) detected no sexual differences in darkness (or whiteness) of underparts over the species' range.

Elsewhere in the species' range, females tend

to have more spotting on primaries, secondaries, and coverts than males (Jackson 1970). We detected no sexual difference in this character, perhaps because populations in western North America tend to have less spotting than eastern populations (Coues 1877, Voous 1947).

P. v. piceoides is unique among western North American *P. villosus* in having dark markings on the belly and flanks, and on the tail (such markings occur occasionally in adults from Vancouver Island, coastal British Columbia, and elsewhere, however; Ridgway 1914, Voous 1947, Ouellet 1977). Similar markings to those of *P. v. piceoides* occur regularly in two other insular populations: Newfoundland (*P. v. terrae-novae*) and Grand Bahamas (*P. v. piger*) (Jenkins 1906, Oberholser 1911). Dorsal barring, markings on the underparts, and markings on the outer rectrices are thought to reflect ancestral states in *Picoides* woodpeckers (Goodwin 1968, Short 1971). Their independent evolution in several insular populations presumably reflects neoteny, as the characters in question occur in juvenal plumage elsewhere in the species' range (Jackson 1971, Ouellet 1977). The sexes do not differ in these attributes on the Queen Charlotte Islands or Vancouver Island.

TABLE 4. Sexual dimorphism in size (adult specimens only).^a

Variable	Queen Charlotte Islands	Vancouver Island
Body mass (g)	10.0	—
Length, flattened wing (mm)	1.27	2.26
Chord, exposed culmen (mm)	12.2	12.0
Chord, bill tip to anterior edge of nares (mm)	12.6	11.4
Tarsal length (mm)	4.74	2.68
Tail length (mm)	-1.08	0.74
Chord, claw IV (mm)	5.37	4.63

^a Values shown are 100[(male measurement/female measurement) - 1].

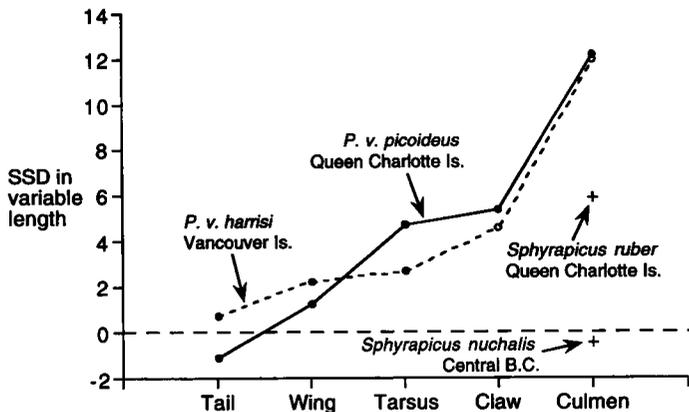


FIGURE 2. Sexual size dimorphism (SSD) in different variables. SSD in length of culmen is greater than in other characters, but does not differ between *P. villosus piceoides* and *harrisi*. Lines join data points to emphasize trends. SSD was computed as $100[(\text{male measurement}/\text{female measurement}) - 1]$. Points for Red-breasted (*Sphyrapicus ruber*) and Red-naped (*S. nuchalis*) Sapsuckers also are shown (see text).

In summary, sexual differences in plumage of *P. v. piceoides* and *harrisi* are small, and the sexes overlap extensively. This pattern is typical of the species throughout its range and has apparently not been evolutionarily altered for life on the Queen Charlotte Islands or elsewhere.

P. v. piceoides is similar in size to other populations in the Pacific Northwest, including coastal and more southern populations in British Columbia and more northern coastal populations in southeastern Alaska (Jackson 1970, Ouellet 1977). Thus, no evolutionary differentiation in the species' size appears to have taken place on the Queen Charlotte Islands, except in the smaller bill.

Sexual dimorphism in woodpeckers is sometimes greatest in simple communities (e.g., islands), where ecological release in feeding ecology is possible, or where high population densities (with attendant increased intraspecific competition) often occur (Selander 1966, 1972, Stamps et al. 1997). Examples are the Cuban Green Woodpecker (*Xiphidiopicus percussus*), Hispaniolan Woodpecker (*Melanerpes striatus*), and Puerto Rican Woodpecker (*M. portoricensis*). Increased sexual dimorphism in woodpeckers on islands is manifested in the feeding apparatus, with males evolving larger tongues and bills, females smaller tongues and bills, or both (Selander 1966, 1972). The Hairy Woodpecker should show similar patterns because males and females differ in foraging behavior and bill size (Kilham 1965, Selander 1965). On the Queen Charlotte Islands, in particular, ecological release might be expected, as only Hairy Woodpecker, Northern Flicker (*Colaptes auratus*), and Red-breasted Sapsucker (*Sphyrapicus ruber*) occur there (Short 1982, Cowan 1989). On Vancouver Island those species plus Downy (*Picoides pubescens*), Pileated (*Dryocopus pileatus*), and Lewis' (*Melanerpes lewisi*) Woodpeckers reside or breed (the latter species only in the southern part, however; Godfrey, 1986). Contrary to prediction, sexual dimorphism is similar in all characters—including the bill—in *P. v. piceoides* and *harrisi* (Fig. 2). Interestingly, slight (~ 6%) sexual size dimorphism in length of bill occurs in the normally monomorphic Red-

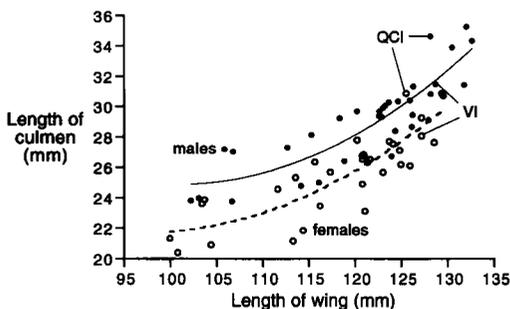


FIGURE 3. The bill is relatively longer in large-bodied (estimated by wing length) populations of *P. villosus*. Data represent geographic samples from throughout the species' range. Curves represent quadratic regressions: for males (solid circles), $Y = 104.6 - 1.60X + 0.008X^2$ ($r^2 = 0.75$); for females (open circles), $Y = 72.8 - 1.11X + 0.006X^2$ ($r^2 = 0.72$).

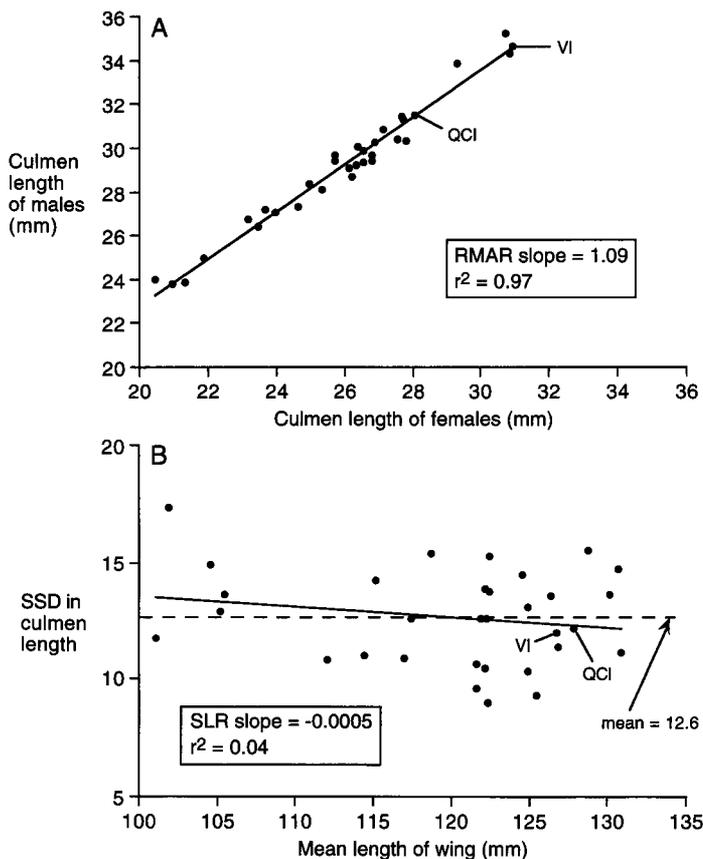


FIGURE 4. Sexual dimorphism in relative bill size of *P. villosus* does not vary geographically. A—bivariate plot of chord of exposed culmen in males and females for geographic samples from throughout the species' range; regression line from reduced major axis regression (RMAR) is shown. B—sexual size dimorphism {SSD = 100[(male/female) - 1]} in chord of exposed culmen plotted against mean length of flattened wing [= (male + female)/2], for geographic samples from throughout the species' range; regression line from simple linear regression (SLR) is shown (data from Ouellet [1977] and this study).

breasted Sapsucker on the Queen Charlotte Islands, which seems to be the only place in the species' range where such a sexual difference exists (Walters and Miller 1999). The Northern Flicker on the Queen Charlotte Islands merits study from this viewpoint, as the "purest" red-shafted forms may occur there in isolation from mainland populations (Short 1965, Moore 1995).

The absence of a large sexual difference in length of bill in *P. v. piceoides* initially seems surprising, considering the isolation of the Queen Charlotte Islands, their simple avifauna, and the subspecies' distinctiveness. This finding is consistent with conservatism in sexual size dimorphism in the species, however, as revealed

at several levels of analysis. First, as noted above, bill size of *P. villosus* is uncorrelated with body size in both sexes of the QCI and VI samples. It is usual for scaling relationships such as this one to become stronger at higher taxonomic levels (Gould 1966, Peters 1983, Calder 1984), and this is true here: across a broad range of geographic samples, bill size increases disproportionately with body size in both males and females (Fig. 3). Bill size between the sexes is highly correlated at this level of analysis (Fig. 4A), so sexual size dimorphism is uniform across populations—despite the wide range in body size and ecological conditions represented by the samples (Fig. 4B) (contrast Hogstad 1993). Selander (1966) analyzed sexual size di-

morphism across species of melanerpine woodpeckers in a similar manner, and likewise found no evidence of a relationship to body size.

Refugia were present in Kodiak Island, southeastern Alaska, the Queen Charlotte Islands, and Vancouver Island during the last glacial maximum about 17,000–20,000 years ago (Kavanaugh 1992). Vegetation then was tundra, hence was unsuitable as woodpecker habitat (Hebda 1995). Thus, Hairy Woodpeckers in the Pacific Northwest presumably colonized coastal Alaska and British Columbia (including the Queen Charlotte Islands) from south of the ice sheet. The subspecies *P. v. picoideus* differentiated into its present distinctive form over the last ~12,000 years, when suitable forested habitat first appeared on the Queen Charlotte Islands (Mathewes 1989, Hebda 1995).

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