

WING MORPHOLOGY VARIES WITH AGE BUT NOT MIGRATORY HABIT IN AMERICAN DIPPERS

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ABSTRACT.—We investigated variation in morphology of American Dippers (*Cinclus mexicanus*) in the Chilliwack River watershed, British Columbia in relation to gender, age and migratory habit. Male dippers had linear dimensions that were 2–9% longer and, on average, were 16% heavier than females. Adults (AHY) were the same structural size as yearlings (HY). Yearlings, however, had shorter and more rounded wings than adults providing support for the hypothesis that an increased vulnerability to predation may lead to selection for traits that improve take-off performance and maneuverability. Yearlings also had shorter tails suggesting other selective pressures shape tail morphology. Dippers in this population may be sedentary or migrate short distances to breed at higher elevations. We found no evidence that wing or tail morphology varied with migratory habit or that sedentary dippers, that have higher reproductive success, are larger or heavier than migrants. *Received 1 November 2007. Accepted 11 May 2008.*

Migration can impose strong selection pressure on traits that influence speed and efficiency of long-distance flight, and may have a major role in maintaining inter- and intra-specific variation in wing morphology (Alerstam and Lindström 1990, Alerstam 1991). Aerodynamic theory suggests that costs of long-distance flight are reduced if wings are longer and more pointed, and tails are relatively short (Rayner 1988, 1990; Norberg 1990, 1995). Comparative studies have confirmed that migratory species typically have more pointed wings than sedentary species (Marchetti et al. 1995, Mönkkönen 1995, Lockwood et al. 1998). Some within species comparisons have reported wing length and/or wing pointedness increase with migration distance (Pérez-Tris and Tellería 2001, Fielder 2005, O'Hara et al. 2006), and migratory populations have longer and more pointed wings than sedentary populations (Copete et al. 1999, Pérez-Tris and Tellería 2001). Intra-specific differences in wing morphology can evolve rapidly. For example, House Finches (*Carpodacus mexicanus*) introduced into eastern North America in 1940 soon became migratory (Able and Belthoff 1998) and, by 2002, had more pointed wings than sedentary House Finches in western North America (Egbert and Belthoff 2003).

Other studies have found that wing length or pointedness is not correlated with migration distance or migratory behavior (Keast 1980; Mulvihill and Chandler 1990, 1991; Burns 2003). These results may occur because avian flight apparatus is also shaped by other, potentially opposing, selection pressures. For example, predation may select for shorter rounder wings that improve take-off performance (Norberg 1990, Swaddle and Lockwood 2003), and shorter rounder wings and longer tails that enhance maneuverability (Norberg 1990). This may explain why juvenile birds, which are more vulnerable to predators, typically have shorter and more rounded wings than adults (Alatalo et al. 1984). Avian flight apparatus may also be shaped by use of differing foraging strategies, habitat selection, prey size, or sexually selected courtship behaviors (Norberg 1979, Winkler and Leisler 1985, Hedenstrom and Möller 1992, Marchetti et al. 1995, Stiles et al. 2005).

American Dipper (*Cinclus mexicanus*) populations in mountainous areas are composed of sedentary individuals (residents) that occupy multi-purpose territories year round and migratory individuals (migrants) that overwinter with residents but migrate short distances to higher elevation territories to breed (Morrissey et al. 2004). Long-term monitoring of marked birds has shown that individual dippers rarely switch strategies (Gillis et al. 2008).

We investigated whether migratory and sedentary American Dippers differ in mor-

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phology before or after their first complete (adult) prebasic molt. Specifically, we examined whether (1) short-distance altitudinal migrants have longer more pointed wings and shorter tails than residents, (2) yearlings have shorter more rounded wings than adults, and (3) if residents, that consistently have higher reproductive success (Gillis et al. 2008), are larger than migrants.

METHODS

Study Area and Field Procedures.—We studied American Dippers in the Chilliwack River watershed ($49^{\circ} 0' N$, $121^{\circ} 4' W$), 100 km east of Vancouver in southwestern British Columbia, Canada. We worked at eight sites (each 2 km long) on the main stem of the river and seven sites on tributaries (sections on tributaries ranged from 0.5 to 6.5 km in length). Adults were captured in mist-nets and banded with unique combinations of three color bands and a metal USGS band. We weighed all birds captured between October 2004 and June 2007 to the nearest 0.5 g using a Pesola spring balance. We measured unflattened wing chord and tail lengths to the nearest 1 mm using appropriate rulers. We measured tarsus length (from the back of the tarsal joint to the most distal scale), and the distance from the back of the head to the tip of the bill to the nearest 0.05 mm using dial calipers. We also measured distances between the wing-tip and the tip of each primary feather from the first to the ninth (primary distances 1 to 9, numbered ascendantly from the leading edge of the wing) to the nearest 0.1 mm using dial calipers for birds captured between October and February 2004–2005 and 2005–2006. We calculated primary lengths (P1–P9) as the distance from the carpal joint to the tip of each primary on the folded wing following Ewer (1990). All primary measures were taken by DJG. We only used one set of measurements per bird in analyses (selecting the data where feathers were least worn) unless birds were measured as both yearlings and adults when two sets of measurements were included ($n = 5$).

We differentiated between first-year (HY = yearlings) and older birds (AHY = adults) on the basis of plumage characteristics (Pyle 1997). Yearlings that retain some juvenile feathers after their partial post-juvenile molt

have relatively abraded, narrow, brownish-gray primary coverts. Yearlings may also have a contrast or molt limit between retained juvenal and molted feathers among the greater coverts. Adults that complete the post-nuptial molt have broader, more truncate primary coverts that are slate-gray with whitish tips when fresh. Age separation was difficult in 10 cases and these individuals were classified as being of unknown age.

We classified gender of birds captured during the breeding season based on presence of a brood patch and behavior (only female American Dippers incubate eggs and brood young; Kingery 1996). Birds captured during fall and winter 2004–2005 and 2005–2006 were classified to gender using a DNA-based test that relies on PCR amplification of a section of the CHD1 genes (CHD1-W and CHD1-Z) on the avian sex chromosomes following Griffiths et al. (1998). The DNA used was isolated from small blood samples (10–70 μ l) collected at banding. Behavioral and molecular methods of gender identification were consistent ($n = 22$).

We classified individuals as being residents or altitudinal migrants. Residents were sedentary, and over-wintered and attempted to breed at the site where they were captured. Migrants were those that (1) bred on tributaries at least 2 km from wintering sites on the river and left these territories after the breeding season, or (2) wintered on the Chilliwack River but left prior to breeding. Individuals captured on the main stem of the river outside the breeding season could not be assigned a migratory strategy unless they were known to survive the winter (i.e., were observed during or after February).

Statistical Analyses.—We examined variation in the wing morphology of American Dippers following Lockwood et al. (1998). This multivariate technique uses a size-constrained components analysis (SCCA) to produce three independent measures of wing morphology; overall wing size, wing pointedness, and wing convexity (i.e., the shape of the proximal part of the wing). We subsequently used general linear models to investigate morphological variation. We evaluated gender, age and migratory habit effects on eight variables; (1) head-bill length, (2) tarsus length, (3) wing chord length, (4) tail length,

TABLE 1. Loading and variance explained by three components from a SCCA of primary lengths in American Dippers. Primaries 1 to 9 are numbered ascendantly from the distal leading edge of the wing. Shape variance is the partitioning of variance after the isometric size variance explained by wC1 is removed.

Primary/variance	wC1	wC2	wC3
1	0.34	-0.51	-0.36
2	0.34	-0.31	-0.08
3	0.34	-0.31	0.02
4	0.33	-0.15	0.03
5	0.33	0.02	0.25
6	0.33	0.11	0.28
7	0.33	0.24	0.35
8	0.33	0.36	0.25
9	0.34	0.57	-0.73
% total variance explained	96.9	1.6	0.7
% shape variance explained		57.0	23.0

(5) body mass, (6) overall wing size, (7) wing pointedness and (8) wing convexity. We initially fitted a full model in all analyses and sequentially removed all non-significant terms until only significant factors remained. No interactions were significant (all $P > 0.05$) and we report the change in the variance ratio ($\Delta v.r.$) when main effects are dropped from the final model.

RESULTS

We captured 181 birds between October 2004 and June 2007, measuring primary distances for 92 birds captured between October and February 2004–2005 and 2005–2006. Twenty of these birds were caught on more than one occasion, fifteen being captured twice in the same year. Recaptured birds included migrants and residents of both age classes. The SCCA produced three components that explained >95% of the variation in primary feather lengths (Table 1). The first component (wC1) measured isometric size with all primaries contributing equally to the wC1 score. The second component (wC2) explained 57% of the variation in wing shape and was a good measure of wing pointedness. The more negative the wC2 score, the more pointed the wing as the outer primaries had negative loadings and the inner primaries had positive loadings. The third component (wC3) measured wing convexity with higher scores being associated with longer primaries in the center of the wing (P5–P8), and shorter primaries at the proximal and distal edge (P1 and P9; Table 1).

Effects of Gender and Age on Morphology.—American Dippers were sexually dimorphic; males had linear measures 2–9% longer than females, and were 16% heavier (Table 2). Adults were the same structural size and mass as yearlings of the same gender, but had longer wing chords and longer tails (Table 2). Adults and yearlings had wings that were the same overall size (wC1), but their wings differed in shape (Table 2). Adult dippers had a lower wing pointedness score (wC2) than yearlings, which corresponds to having longer primaries at the leading edge of the wing and shorter primaries at the inner edge of the wing. Adults and yearlings did not differ in wing convexity scores (wC3; Table 2).

Age-related differences in wing and tail length remained after controlling for the amount of time elapsed since primary and tail feather growth was completed (estimated as 1 Jun for yearlings and 1 Sep for adults; wing chord, age effect: $\Delta v.r. = 10.3, P = 0.002$, time effect: $\Delta v.r. = 6.7, P = 0.01$; tail length, age effect: $\Delta v.r. = 20.0, P < 0.001$; time effect: $\Delta v.r. = 0.4, P = 0.71$). Wing chord and tail length did not change between captures for 15 individuals captured more than once in the same year (mean change \pm SE: wing chord -0.1 ± 0.3 mm, $t = -0.52, P = 0.61$; tail length 0.4 ± 0.3 mm, $t = 1.25, P = 0.23$) and differences were not correlated with time interval between captures (wing chord $r_p = -0.2, P = 0.43$; tail $r_p = -0.1 P = 0.60$).

Migratory Habit and Morphology.—Sedentary and migratory dippers were the same size. Head-bill length, tarsus length, wing

TABLE 2. Morphological variation of American Dippers ($\bar{x} \pm SD$) in relation to gender and age. Gender and age effects are the change in the variance ratio ($\Delta v.r.$) when age or gender is dropped from general linear models containing significant main effects.

Character	Male		Female		$\Delta v.r.$	P	Age effect
	Yearling	Adult	Yearling	Adult			
Head-bill length, mm	47.3 \pm 0.8	47.6 \pm 0.9	45.9 \pm 0.6	45.8 \pm 0.8	182.7	<0.001	2.4
Tarsus length, mm	34.6 \pm 0.9	34.8 \pm 0.8	32.6 \pm 0.8	32.4 \pm 0.9	258.9	<0.001	0.02
Wing chord, mm	90.7 \pm 2.5	91.7 \pm 2.7	83.8 \pm 1.6	84.4 \pm 1.9	357.2	<0.001	5.4
Tail length, mm	49.0 \pm 2.4	51.1 \pm 2.6	45.8 \pm 1.9	47.3 \pm 2.1	89.5	<0.001	25.7
Mass, g	57.0 \pm 5.1	57.2 \pm 6.4	49.3 \pm 4.7	48.6 \pm 5.1	95.4	<0.001	0.2
<i>n</i>	44	61	38	27			0.69
Wing size, wc1	1.5 \pm 2.0	1.8 \pm 2.0	-3.2 \pm 1.3	-3.3 \pm 1.8	151.4	<0.001	0.05
Wing pointedness, wc2	0.0 \pm 0.4	-0.2 \pm 0.3	0.2 \pm 0.3	-0.2 \pm 0.5	1.3	0.27	0.83
Wing convexity, wc3	0.0 \pm 0.2	0.0 \pm 0.2	0.0 \pm 0.1	0.0 \pm 0.2	0.7	0.41	<0.001
<i>n</i>	24	28	18	11			0.45

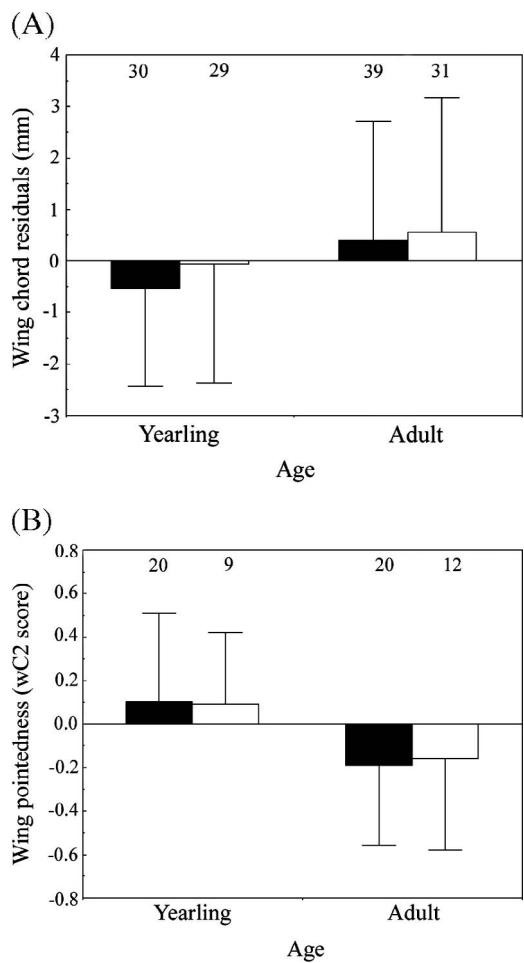


FIG. 1. Relationship between age and (A) residual wing chord length \pm SD and (B) wing pointedness \pm SD of migratory and sedentary American Dippers. Migrants are represented by black bars, residents by white bars. Wing chord residuals are unstandardized residuals after controlling for gender. Numbers denote sample sizes for each category.

chord length (Fig. 1A), tail length and overall wing size of an individual, after controlling for gender and age effects, were all unrelated to their migratory habit (Table 3). Sedentary dippers also had the same wing shape as migratory dippers; neither wing pointedness (Fig. 1B), nor wing convexity varied with migratory habit (Table 3).

DISCUSSION

Inter- and intra-specific studies have shown that migration can influence wing length and

TABLE 3. Morphological variation of American Dippers in relation to migratory habit. LS means \pm SE are presented after controlling for significant age and/or gender effects. Sample sizes are the same as in Table 2. We report the change in the variance ratio (Δ v.r.) when migratory habit is dropped from general linear models containing significant main effects.

Character	Resident	Migrant	Δ v.r.	<i>P</i>
Head-bill length, mm	46.8 \pm 0.1	46.9 \pm 0.1	1.1	0.29
Tarsus length, mm	34.0 \pm 0.1	34.0 \pm 0.1	0.4	0.52
Wing chord, mm	87.9 \pm 0.3	87.7 \pm 0.3	0.4	0.53
Tail length, mm	48.5 \pm 0.3	49.0 \pm 0.3	0.8	0.37
Mass, g	52.6 \pm 0.8	53.1 \pm 0.7	0.2	0.66
Wing size, wC1	0.1 \pm 0.4	0.2 \pm 0.3	0.0	0.99
Wing pointedness, wC2	-0.1 \pm 0.1	-0.1 \pm 0.1	0.01	0.91
Wing convexity, wC3	-0.01 \pm 0.02	-0.04 \pm 0.03	0.9	0.35

shape, but our study indicates that selection pressures imposed by migration did not influence the morphology of yearling or adult American Dippers. Sedentary and migratory dippers may have similar wings and tails because altitudinal movements of migrants do not impose sufficient selection pressure on these morphological traits. Migratory dippers in this population move relatively short distances (max observed = 21 km; DJG, unpubl. data) compared to other species where migration related differences in morphology have been detected. For example, migratory Eurasian Blackcaps (*Sylvia atricapilla*) that have longer wings than sedentary birds travel between 100 and 1,700 km (Pérez-Tris and Tellería 2001). Similarly, migratory House Finches in eastern North America that differ morphologically from their sedentary counterparts in western North America migrate between 80 and 1,000 km (Able and Belthoff 1998).

Alternatively, the flight morphology of residents and migrants may not differ because gene flow between the two groups counters any effect of selection. We have no molecular data with which to evaluate the level of genetic isolation between residents and migrants. Some gene flow is likely, even though residents and migrants breed in different locations because young may not adopt the same migratory habit as their parents (Gillis et al. 2008). Morphological differences between residents and migrants would still be expected, even with moderate levels of gene flow, if intra-specific competition affects which individuals are residents and, thus, enjoy higher reproductive success. However, we found no evidence that residents were larger

or heavier than migrants. Further work is required to assess how genetic and environmental factors affect the migratory habit of American Dippers.

Predation can lead to selection for shorter rounded wings that allow birds to accelerate faster and take-off at a steeper angle, and longer tails that can provide additional lift and enhance maneuverability (Norberg 1990, Thomas and Balmford 1995). Yearling dippers in our study had shorter rounder wings than adults, consistent with the hypothesis that predation can influence wing shape and that differences in vulnerability to predation can lead to age-dependent variation in wing morphology (Alatalo et al. 1984). However, yearlings had shorter tails than adults. Tails of birds are often co-opted for other functions because tails generate less lift than wings and the aerodynamic performance of tails is less impacted by changes in size and shape (Thomas and Balmford 1995). Diving and swimming underwater may exert stronger selection pressure on tail length than flight in dippers, and age-dependent variation in tail length may arise if longer tails compromise the acquisition of these skills in young birds.

Age-related differences in both wing or tail length could arise because yearlings do not replace their primary and tail feathers in their post-juvenile molt, and their feathers are consequently more worn. This appears unlikely as age-related differences remained after controlling for the amount of time elapsed since primary and tail feather growth was completed. Alternatively, yearling dippers may have shorter wings and tails than adults because of nutritional constraints on juvenile feather de-

velopment (van Balen 1967). We are currently unable to rule out this hypothesis.

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