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SEASONAL TRENDS IN POPULATION DENSITY, DISTRIBUTION, AND MOVEMENT OF AMERICAN DIPPERS WITHIN A WATERSHED OF SOUTHWESTERN BRITISH COLUMBIA, CANADA

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Abstract. American Dippers concentrate on low-elevation streams during fall and winter in many parts of their range; however the breeding origin relative to the wintering location is poorly understood. Our objectives were to identify seasonal changes in the density and distribution of American Dippers, to classify the migratory behavior of the local population, and to determine the origin of winter migrants within a coastal watershed of British Columbia, Canada. During 1999–2002, we color banded 522 dippers and radio-tagged 14 in the Chilliwack River watershed. Using mark-resighting techniques, we identified peak densities on the main river during early November (9.8 ± 1.4 [SE] birds per stream km), which was nearly 5 times higher than in early July (2.1 ± 0.3 birds per stream km). The watershed's total population size, estimated from November surveys, was 429 ± 64 [SE] dippers in 1999, 682 ± 79 in 2000, 697 ± 123 in 2001, and 550 ± 72 in 2002. The majority (79–90%) of the dipper population seasonally migrated, primarily moving from the main river in fall and winter to the higher-elevation tributaries in spring. The remaining dippers (10–16%) remained resident on the main river year-round. Migrants showed a high degree of winter site fidelity with 67% returning to the same site on the Chilliwack River for 2 or more years. Given the population's defined structure and predictable seasonal movements, this study has implications for applying American Dipper populations as indicators of water and habitat quality in North American watersheds.

Key words: altitudinal migration, American Dipper, Cinclus mexicanus*, indicator species, mark-recapture, radio-telemetry, watershed.*

Tendencias Estacionales en Densidad Poblacional, Distribución y Movimiento de *Cinclus mexicanus* en una Cuenca del Sudoeste de la Columbia Británica, Canadá

Resumen. *Cinclus mexicanus* se concentra en ríos ubicados a baja elevación en muchas partes de su rango durante el otoño y el invierno; sin embargo, se conoce poco sobre la relación entre el sitio originario de reproducción y la localización durante el invierno. Nuestros objetivos fueron identificar los cambios estacionales en la densidad y la distribución de *C. mexicanus*, clasificar el comportamiento migratorio de la población local y determinar el origen de los migrantes invernales en una cuenca costera de la Columbia Británica, Canadá. Entre 1999 y 2002 anillamos con bandas de color 522 individuos de *C. mexicanus* y seguimos con radio-telemetría 14 individuos en la cuenca del Río Chilliwack. Usando técnicas de marcado y re-avistamiento, identificamos densidades pico en el río principal durante principios de noviembre (9.8 ± 1.4 [EE] aves por km de río), lo que fue casi 5 veces más alto que a principios de julio (2.1 ± 0.3 aves por km de río). El tamaño total de la población de la cuenca, estimado a partir de los censos de noviembre, fue 429 ± 64 [EE] aves en 1999, 682 ± 79 en 2000, 697 ± 123 en 2001 y 550 ± 72 en 2002. La mayoría (79–90%) de la población de *C. mexicanus* migró estacionalmente, moviéndose principalmente desde el río principal en el otoño y el invierno a los tributarios de mayor elevación en la primavera. Los individuos restantes (10–16%) permanecieron como residentes en el río principal durante todo el año. Los migrantes mostraron un alto grado de fidelidad a los sitios de invierno, con un 67% de los individuos retornando al mismo sitio en el Río Chilliwack por 2 años o más. Dada la estructura definida de la población y los movimientos estacionales predecibles, este estudio señala que las poblaciones de *C. mexicanus* pueden ser usadas como indicadores de la calidad del agua y del hábitat en las cuencas de América del Norte.

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INTRODUCTION

Monitoring programs involving birds as indicators of habitat quality are now widely used on both a local and national scale as an effective way to measure spatial and temporal trends in degradation of key ecosystems (Furness 1993). In general, knowledge about the ecological impacts on monitored populations may serve as an early warning of habitat degradation. However, a solid understanding of the basic ecology of an indicator species is necessary to effectively interpret population-level effects and monitor key ecosystems.

Numerous European studies have successfully used the Eurasian Dipper (*Cinclus cinclus*), an aquatic songbird, as an environmental monitor of riparian habitat including changes in water quality (Ormerod et al. 1991, Tyler and Ormerod 1992, Logie et al. 1996, Buckton et al. 1998, Sorace et al. 2002). Eurasian Dipper populations show considerable variability in migratory tendency, with some more northern populations demonstrating clear seasonal movement while others are more sedentary (Tyler and Ormerod 1994). In North America, recent studies have also supported the use of the American Dipper (*Cinclus mexicanus*) as a biological indicator of stream condition (Feck 2002, Strom et al. 2002, Morrissey et al. 2004). However, relatively little is known about the migration ecology of the North American species. If the American Dipper is to be a successful indicator of changes in environmental quality, the population's structure and movement patterns need to be understood.

Most accounts of partial migration in the Eurasian and American Dipper have been primarily descriptive or speculative in nature (Bent 1948, Bakus 1959a, 1959b, Balát 1962, Jost 1969, Whitney and Whitney 1972, Tyler and Ormerod 1994). Furthermore, the extent of migration and the location of the wintering and breeding sites of individual American Dippers have never been examined. In Canada, few records exist on the American Dipper's abundance and no comprehensive ecological studies have been done on this species in British Columbia, despite the fact that the majority of the Canadian population exists here (Campbell et al. 1997). Observations in southwestern British Columbia have indicated high densities of American Dippers occur in fall and winter on several rivers and streams, which is consistent with reports from elsewhere in the species' range (King et al. 1973, Kingery 1996, Campbell et al. 1997). Speculations as to the origin of these wintering birds include a possible migration from more northern latitudes where seasonal freezing is common (Campbell et al. 1997) or an altitudinal migration from remote mountain streams (Kingery 1996). Lack of research in this area has precluded our understanding of the population dynamics and movement patterns of the American Dipper. However, the use of marked individuals may facilitate relating wintering populations to specific breeding origins.

This research addresses several questions about the migratory movements of American Dippers and temporal trends in dipper population density, distribution, and size. Our objectives were to document the seasonal changes in density and distribution of dippers within a watershed of southwestern British Columbia; to identify the composition and size of the local population; and to determine the origin and movement patterns of winter migrants through extensive banding and radio-telemetry.

METHODS

STUDY AREA

The study area is located within the Chilliwack River watershed (49°0′N, 121°4′W), a tributary of the large Fraser River system, located approximately 100 km east of Vancouver in the Cascade Range of southwestern British Columbia, Canada (Fig. 1). The Chilliwack River is 43.5 km in length. It is fed by a large glacial lake at its upper end and converges into the Vedder River downstream. The watershed ranges from 20 to 2500 m elevation and drains an area of over 1200 km^2. The watershed tributaries are first through third order streams, and the river is dominantly a fourth or fifth order stream. This watershed served as a suitable study site because of its high winter densities of American Dippers, as observed in several watersheds throughout the region, as well as good road accessibility. The Chilliwack River and its tributaries are characterized by highly suitable dipper habitat composed of fast-moving water, a variety of riffles and pools, large boulders and cliffs, and a mixture of cobble and sand substrate.

CAPTURE AND MARKING

From 1999 to 2002, we captured and marked 522 American Dippers in our study area in ac-

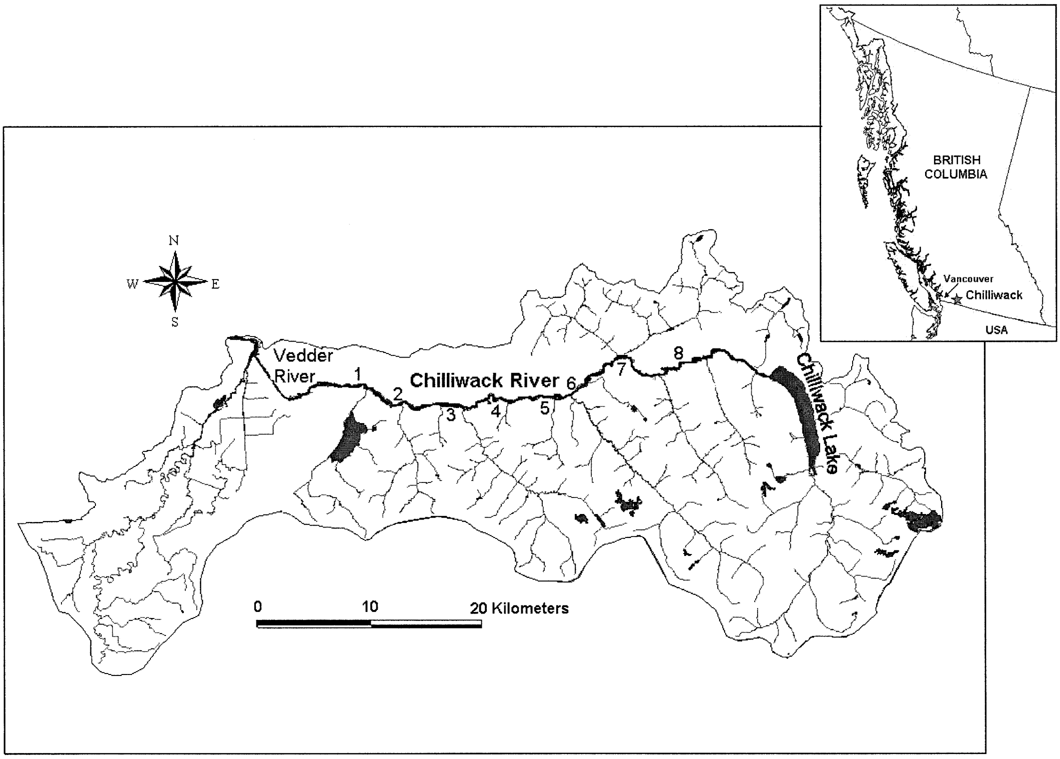

FIGURE 1. Map showing the Chilliwack River watershed in southwestern British Columbia, Canada. Numbers (1–8) on the watershed map indicate the locations of winter banding and bimonthly survey sites along the main stem of the Chilliwack River. Shaded areas indicate open water lakes and streams.

cordance with federal scientific, banding, and animal care permits. We established eight sites along the river at approximately 4-km intervals for trapping and surveying (Fig. 1). The majority of dippers were caught at those eight sites from January to March, as they wintered on the Chilliwack River. Additional breeding birds were caught opportunistically until late July in all areas of the watershed including the tributaries. We trapped adult and newly fledged dippers primarily by flushing them into 6-m passerine mist nets set up over moving water in narrow channels or on edges of the river and creeks. A hand net was used to trap a few additional adults while on the nest during incubation (females) or during nest building (males). Capture and handling of breeding birds was never observed to cause nest abandonment or hatching failure. In 1999, 2000, and 2001, nestling dippers were banded when they were 12–14 days old. Nests were monitored weekly throughout the breeding season to allow for accurate ageing of nestlings. All dippers were weighed, measured, and banded with a numbered USFWS aluminum band and three colored celluloid bands. Adult dippers are sexually dimorphic in size and have different breeding behavior, allowing us to sex them by wing chord measurement, by the presence of a brood patch during the breeding season, or by incubation behavior (only females incubate) (Kingery 1996). Dippers in juvenile plumage cannot be sexed in the hand but were later identified if captured or sighted in the following year.

SURVEYS

Beginning in November 1999 and then every 2 months until November 2002, we surveyed the eight sites along the main stem of the Chilliwack River. The search area at each of the eight sites consisted of approximately 2 km of linear stream segments (precise distances were determined using Bushnell Yardage Pro 400 rangefinders, Richmond Hill, Ontario, Canada). Surveys were routinely done within the first 2 weeks of the month by two experienced observers (including CAM). Both observers walked along the riverbank searching all channels and the lower reaches of creeks where they met the river. The same search areas were used for all surveys. Each survey took 3 consecutive days to complete, moving upstream for each of the eight sites such that we completed three sites each on days one and two and the last two sites on day three. Although it is possible that individual dippers could have moved between sites during subsequent days of the counts, we never encountered any double observations of banded birds between sites during any of the surveys. We made periodic visits to the river in late summer but did not survey in early September because the majority of birds were molting and therefore not visible for counting.

We searched for all dippers and recorded all banded and unbanded birds. In addition, if we sighted a bird but were unable to identify whether it was banded or not (usually because it was flying out of range), it was recorded as unknown but included in the total count. The unique band combinations were visible with 8× binoculars or a 10–40× spotting scope when the birds stood on rocks, even at distances of 100 m or more. Throughout the 4-year study, and particularly during the field seasons from January to July, we searched for dippers throughout the watershed and recorded any observations of banded individuals. When we sighted a dipper, we made every effort to identify whether it was banded. We kept a history for each banded bird, including the date and location of all sightings as well as any relevant breeding information.

Since most of the breeding birds on the river were color banded, we were able to divide the population into two groups: dippers that remained on or near their breeding territories year-round, usually on the river main stem (river residents); and dippers that seasonally migrated or dispersed, moving more than 1 km between their wintering site on the river and a defined breeding territory, typically on a tributary (creek migrants). Since we could not assume this was a closed population, other nonresidents that wintered on the river but moved to an unknown breeding site either within or outside the watershed were also classified as migrants.

RADIO-TELEMETRY

In late February and early March of 2000, we radio-tagged 14 adult dippers wintering along the main river channel. Six birds had been captured and color banded in 1999 and had moved off the river in spring, while eight had not been previously marked. We used transmitters with a whip antenna (Holohil Systems Ltd., Carp, Ontario, Canada) that had unique frequencies and weighed approximately 1.65 g, which is approximately 2.5–3.5% of a dipper's body weight. We glued the transmitters to several contour feathers with a waterproof epoxy (Titan Corp., Lynnwood, Washington) approximately 1 cm anterior of the uropygial gland on the rump, allowing the radio to fall off over time or when the birds molted. We observed birds feeding and preening normally for several days following transmitter attachment, and resighted four surviving individuals the subsequent winter without their radios. Transmitter batteries had an expected life span of 12 weeks.

We located radio-tagged dippers on the river during late winter and early spring until we could no longer detect a signal using ground-tracking methods. During two aerial telemetry flights (17 April and 7 May 2000), we flew all sections of the watershed following the river and its tributaries to the snowline to try to locate all 14 radio-tagged birds. From the air, we detected transmitter signals from several km away, but on the ground, transmitters had limited range of 1–2 km due to the mountainous terrain.

MOVEMENT AND POPULATION-SIZE ANALYSIS

Movement patterns were analyzed using the multistrata model in Program Mark (White and Burnham 1999). Although the model estimates probabilities for survival, resighting, and movement between independent strata, we report movement estimates only. All dipper resightings throughout the watershed were categorized into eight time periods by breeding season (late March through August) or nonbreeding season (September through early March) and year (1999–2002). Movement patterns were assessed from 668 observations of 298 banded adults during those eight periods. We structured the model with 22 parameters to identify probability of movement between strata during the breeding and nonbreeding seasons with 95% confidence intervals (CI). Males, females, and birds of unknown sex had similar patterns of movement between seasons. Therefore, we pooled the sexes in the model for movement, reporting them as a single probability, but kept them as independent groups for the rest of the model parameters. We designated the river and creeks as independent strata and further treated juveniles as an additional stratum to obtain more accurate estimates of movement probabilities by age. We report the global model and the most parsimonious model as determined by the lowest Akaike's Information Criterion ($QAIC_c$) values adjusted for small sample size and overdispersion.

To estimate the size of the Chilliwack River dipper population, we employed two methods. We first used a ratio estimator (Jolly 1969, Krebs 1999) to calculate population size from the bimonthly surveys. This method did not require any band resighting information but simply used dipper density from the survey counts and an estimate of the total length of stream habitat (an expansion factor) to calculate total population size. Second, we used a Jolly-Seber model in Program Mark (White and Burnham 1999) to estimate the initial population size and rate of change (lambda) from the mark-resighting data. The best model was structured with 12 parameters to keep apparent survival and resighting probabilities different for the breeding and nonbreeding seasons, and to fix a different probability for lambda in each time period. A global model with all parameters free never met convergence due to insufficient data. We used Monte Carlo simulations of analytical estimates of lambda, its covariance matrix, and initial population size taken directly from the Jolly-Seber model, to calculate 95% CI for the population size in each time period. Our main assumption was that the parameter uncertainty was normally distributed for the simulations. The same expansion factor used in the ratio method was then used to scale both the population size estimate and the 95% CI. These confidence intervals were then compared with estimates obtained from the survey counts to confirm their validity. All means are reported ± SE unless stated otherwise.

RESULTS

POPULATION DENSITY AND SIZE

Seasonal dipper movements produced large changes in numbers between river surveys during November to July (Fig. 2). Overall, winter 1999–2000 had the lowest total numbers of birds compared to later winters. Peak densities (number of dippers per km of river) typically occurred along the main river in early November (mean = 9.8 ± 1.4 birds per km), which was nearly five times higher than in early July (mean = 2.1 ± 0.3 birds per km; Fig. 2). Survey means were consistent between years with coefficients of variation for each survey month ranging from 7% to 15%. In 2002, atypical weather likely resulted in an unusual pattern of survey counts for that year.

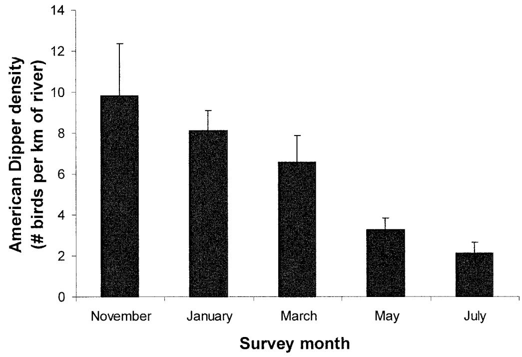

FIGURE 2. Mean density (±SD) of American Dippers (number of birds per kilometer of river) during routine bimonthly surveys (n = 4 years, 1999 to 2002). All surveys were conducted at the same eight sites (Fig. 1) on the main stem of the Chilliwack River, British Columbia, Canada.

Since the majority of our American Dipper population concentrated at low elevations on the main river and at the mouths of creeks in winter, a ratio estimator for density (Jolly 1969, Krebs 1999) proved to be a good method for estimating the total population size for the Chilliwack River watershed. A positive linear correlation existed between the number of dippers counted in November and search distances at each survey site ($r = 0.42$, $P < 0.04$, $n = 4$ surveys, 1999–2002). We estimated the distance of potential wintering areas including the length along the river, the lower reaches of the creeks at their confluence, and all suitable side channels as ~60 linear km. Minimum total dipper population size for the Chilliwack watershed was then estimated as 429 ± 64 birds in November 1999, 682 ± 79 in November 2000, 697 ± 123 in November 2001, and 550 ± 72 in November 2002. Coefficients of variation ranged from 12% to 18%.

The Jolly-Seber model for an open population of marked individuals was used to estimate population size for comparison with the above ratio estimator technique (best model: $QAIC_c$ = 296.34, $\hat{c}$ = 4.77, 12 parameters; all other mod-

TABLE 1. Comparison of Chilliwack River American Dipper population size estimates and 95% confidence intervals for the ratio estimator method (Krebs 1999) and the Jolly-Seber method in Program Mark (White and Burnham 1999). Data are from surverys conducted during 3 days in November (ratio estimator) and from all mark-resighting encounters during the nonbreeding period (Jolly-Seber estimator).

Survey date	Ratio estimate	95% CI	Season	Jolly-Seber estimate	95% CI
November 1998			Non breeding 1998–1999	321	254–388
November 1999	429	295–562	Non breeding 1999–2000	813	567–1059
November 2000	682	518–846	Non breeding 2000–2001	639	393–885
November 2001	697	441–952	Non breeding 2001–2002	425	233–617
November 2002	550	400–700			

els $\Delta QAIC_c > 5$). Simulated 95% CI for the population size estimates overlapped the ratio estimates in 2000 and 2001 but not in 1999 (Table 1). However, the actual Jolly-Seber estimates are not directly comparable with the ratio estimates given that the Jolly-Seber model estimated population size over the entire nonbreeding season and the ratio estimator used only the 3-day November surveys.

COMPOSITION OF THE WINTER POPULATION

Of the 522 individual dippers that were captured and banded during the 4-year study, 250 were adults and 272 were nestlings or fledglings (Table 2). Since most of the breeding birds on the river were color banded, we were able to distinguish the river residents from the creek migrants (Fig. 3). A small proportion of wintering birds (10–16%) remained resident on the river year-round. The remainder of the large winter population (79–90%) was considerably more mobile, routinely moving off the river in early spring (presumably to breed) and returning in the fall. The migratory group consisted of returning banded adults, banded first-year birds, and a large number of unbanded birds. The number of residents remained relatively constant year-round, except in March when there was a marginal increase in new breeders occupying territories on the river (peak breeding density = 2.4–3.0 birds per km). Ultimately, the largest fluctuation in total dipper numbers on the river was attributed to the arrival of migrants in the fall and winter months and their disappearance in early spring (Fig. 3).

We hypothesized that the large influx of dippers in fall could be a result of juveniles flooding the population prior to spring dispersal. After 3 years of marking 260 nestlings and 12 fledglings (in juvenile plumage) from 165 nests throughout the watershed, 48 of 272 nestlings (18%) were resighted in their first winter or later. Banded first-year birds represented only 1.6% to 5.2% of the winter survey sightings, whereas banded adults made up 19% to 25%. This is despite the fact that annual banding numbers were typically higher for nestlings than adults (Table 2). Therefore, first-year birds from nests within the watershed likely did not comprise the majority of the winter population on the river.

DIPPER MOVEMENT PATTERNS

Of the individuals marked as adults in the first 3 years of the study (1999–2001), 102 of 280 adults (36%) were resighted for two or more winters. Winter migrants showed a high degree of winter site fidelity with 67% (60 of 89) returning to the river for 2 or more years. All but two birds were resighted at their winter capture site. The two that were not sighted at their orig-

TABLE 2. Summary of American Dipper banding effort in the Chilliwack River watershed, British Columbia, Canada, 1999–2002. Birds were classified as adults, fledglings, or nestlings; sexes were pooled.

Year	Banded adults	Banded fledglings	Banded nestlings	Total
1999	81	7	67	155
2000	112	1	142	255
2001	39	4	51	94
2002	18	0	0	18
All years	250	12	260	522

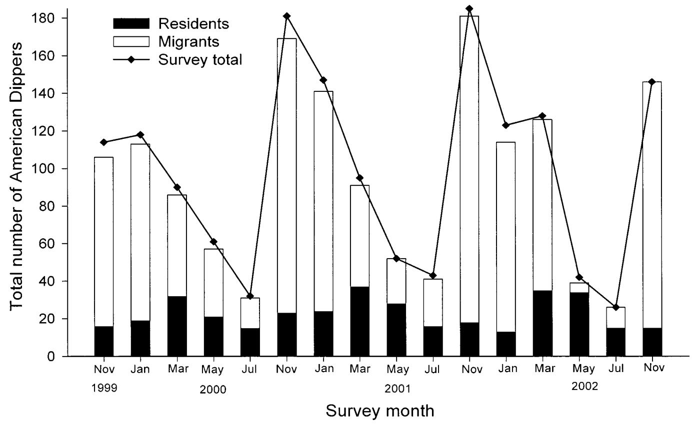

FIGURE 3. Summary of bimonthly surveys on the Chilliwack River, British Columbia, Canada, from November 1999 to November 2002. Line graph indicates survey totals including all banded, unbanded, and unidentified American Dippers sighted on the main stem of the river. Bar graph shows numbers of river residents (birds that breed and winter on the river) and creek migrants (birds that leave the river to breed).

inal capture site were initially captured in March and likely had already started their spring migration.

Analysis of movement between river and creek strata using Program Mark (White and Burnham 1999) revealed that migrant birds moved in spring (from the nonbreeding to breeding season) primarily from the river to the creeks (best model $QAIC_c = 470.55$, $\hat{c} = 4.05$, 22 parameters; global model $\Delta QAIC_c = 437.15$, 192 parameters; all other models $\Delta QAIC_c > 4.9$). In contrast, the movement in the fall (from breeding to nonbreeding season) was primarily from the creeks to the main river (Table 3). Residents generally remained on the river between seasons with little or no movement. Surviving juveniles (n = 10 males, 10 females, 28 unknown sex) that were resighted after their first molt through their first winter moved from their natal site in the breeding season to a wintering location on the river or a tributary. Both male and female juveniles wintered primarily on the main river, in a similar pattern to adult birds. However, juvenile males had a higher probability of moving

TABLE 3. Probability of movement between the Chilliwack River and its creeks by adult and juvenile American Dippers using the multistrata model in Program Mark (White and Burnham 1999). Data show movement in the spring (between nonbreeding and breeding season) and in the fall (between breeding and nonbreeding season) for 1999–2002 combined. Movements for juvenile birds (fledging through first winter) in spring were not estimated since there are no juvenile birds in this period.

Movement parameter	Probability of movement (95% CI)	
	Spring (1999–2002)	Fall (1999–2002)
Adults (both sexes) (n = 298)		
From river to creek	0.21 (0.09–0.43)	0.02 (0.00–0.47)
From creek to river	0.15 (0.01–0.75)	0.53 (0.25–0.79)
Juvenile males (n = 10)		
From natal site to river	—	0.60
From natal site to creek	—	0.40
Juvenile females (n = 10)		
From natal site to river	—	0.88
From natal site to creek	—	0.12
Juveniles unknown sex (n = 28)		
From natal site to river	—	0.50
From nata site to creek	—	0.50

onto a creek in fall than females and juveniles of unknown sex had an equal probability of moving to the river or creeks (Table 3). Following dispersal in the spring, juveniles were identified as adults during all future encounters. Since only 18% of banded nestlings were resighted, our analysis may not be representative of the movement patterns for all juveniles, as many more may have moved outside the study area.

Of the 14 birds with radio-transmitters, we successfully tracked 10 birds for the duration of the battery life. Two birds lost their radios prior to migration and two birds were never relocated in subsequent searches, indicating radio loss, radio malfunction, death, or migration outside the study area. Beginning soon after the radios were mounted in late February and early March, several dippers moved off the winter site for periods of several hours, usually in the morning, and then returned later the same day. Of the 10 birds that retained their radio-transmitters and were tracked to the breeding site, the majority moved from a wintering site on the main river upstream onto a nearby creek and remained within the Chilliwack watershed. The distance moved was highly variable (mean = 5.4 km, range = <1.0 to 16.5 km). The movement of most birds was accompanied by an increase in elevation (mean = 236-m increase, range = 0 to 750 m). The two aerial searches in April and May indicated that the dippers did not move appreciably during the 3-week interval between flights. The majority of movement occurred throughout March. By mid-April, radio-tagged birds had settled on their breeding territories and were not detected or resighted at the winter river sites during telemetry searches, bimonthly surveys, or routine visits until the fall.

DISCUSSION

MOVEMENT PATTERNS

American Dippers in our study watershed were primarily altitudinal migrants, moving upstream in the spring and downstream in the fall. Thus, the mobility of the Chilliwack dipper population produced large changes in density during the annual cycle. Peak densities (7.2–11.6 birds per km) recorded during early November surveys on the river are probably the highest on record for this species. In Boulder, Colorado, the highest densities in October varied from 1.9–4.7 birds per km (Price and Bock 1983). Other British Columbia streams also appear to host high winter densities but lack formal counts of this species (Campbell et al. 1997).

Migratory behavior is consistent with the large changes in seasonal abundance observed in many watersheds of southwestern British Columbia and across the species' range. However, direct evidence in the literature of seasonal altitudinal migration of American Dippers is limited. Price and Bock (1983) gave the only detailed record of dipper movements from a large banded population in Colorado. They found similar increases in seasonal density of dippers in fall moving through their study areas on Boulder Creek and South Boulder Creek. The direction of movement was primarily downstream in fall and upstream in spring. However, they were unable to determine the specific wintering sites of most banded birds. Several other researchers have noted similar shifts in the abundance of American Dippers during the nonbreeding season (Bent 1948, Jewett et al. 1953, Bakus 1959a, 1959b, Whitney and Whitney 1972, King et al. 1973), indicating that altitudinal migration is likely common particularly in the northern part of its range.

Although most of the population migrated seasonally, 10% to 16% of the winter population remained on the river to breed with only a few short absences in late summer or winter. These birds, defined here as river residents, clearly did not follow the same pattern of movement as creek migrants. During winter, the presence of year-round residents as well as altitudinal migrants along the main river channel indicates dippers have a partial migration strategy with two distinct groups occupying the same watershed. While altitudinal migration appears to be the more common strategy among dippers, the presence of resident and migratory American Dippers within a single study area (as for Eurasian Dippers) has been documented infrequently elsewhere (Balát 1962, Price and Bock 1983). Partial migration in dippers likely exists wherever limited stable wintering and breeding habitat are present.

In central and western Europe, including Britain and Ireland, most populations of dippers (*Cinclus c. gularis*, *C. c. hibernicus*, and *C. c. aquaticus*) are largely sedentary. However, regular altitudinal movements in spring and fall are reported for some local populations breeding at high elevations across Europe (Tyler and Ormerod 1994). In Germany, Jost (1969) reported that mainly juvenile and a few adult dippers (*C. c. aquaticus*) in his study area regularly moved between watersheds by flying over ridges. The dippers of Fenno-Scandia and northwest Russia (*C. c. cinclus*), and some birds from the Ural Mountains (*C.c. uralensis*), have been found to migrate up to 1000 km between breeding and wintering areas (Andersson and Wester 1976). Sedentary and migratory strategies in the Eurasian Dipper appear to differ on a local scale and have likely contributed to the large number of subspecies found across Europe.

At least a portion of the marked wintering population in our study area could have arrived from more northern latitudes or were captured while dispersing to other watersheds. However, we have no confirmed records of our banded dippers being sighted outside the Chilliwack watershed. Of our radio-tagged birds, two that were not previously color marked remained on the river and moved very little; however, two others could not be relocated soon after transmitter attachment and were excluded from the results. Since we only mounted 14 transmitters in total and four individuals were not tracked or did not move, our results may have been biased toward shorter movements. Large-scale movements by American Dippers are not commonly reported, but they have been sighted outside their breeding range. Bent (1948) recorded one dipper on the Canadian Plains some 80 km from the mountains. Another dipper sighting on the northwest shore of Lake Superior in Minnesota was estimated to be 1400 km from the nearest breeding habitat, in the Black Hills of South Dakota (Green 1970, Muelhausen 1970). Price and Bock (1983) reported the longest movement of a banded nestling was 75 km (straight-line distance) from its natal site. Among the well-studied Eurasian Dipper populations, roughly 25% of female natal dispersal involves interbasin movements (S. Ormerod, pers. comm.). Watershed populations are probably not isolated, and regular migration in addition to juvenile dispersal across watersheds likely contributes to genetic mixing among American Dippers.

INITIATION OF MIGRATION

Speculation as to what initiates altitudinal migration in dippers and other alpine-breeding birds has been limited. Several other bird species including Dark-eyed Juncos (*Junco hyemalis*; Rabenold and Rabenold 1985), Spotted Owls (*Strix occidentalis*; Laymon 1989), Mountain Bluebirds (*Sialia currucoides*), and White-tailed Ptarmigan (*Lagopus leucurus*; Martin 2001) also seasonally migrate between breeding and wintering elevations. Price and Bock (1983) determined that ice at higher elevations was the ultimate cause of downstream migration in his Colorado dipper population. In our Pacific Northwest population, the initiation of downstream migration from the breeding site to the wintering site occurred in early fall, which is well before freezing and high-elevation winter conditions would force birds to move. Additionally, most creeks in our study area remained open year-round except at the very highest elevations.

One possible explanation for this behavior is that birds move in anticipation of cold stress during winter (Martin 2001). Variation in climate and habitat within a few vertical kilometers can be comparable to variation over thousands of kilometers of latitudinal travel (Rabenold and Rabenold 1985). It would therefore be advantageous to move to lower elevations in autumn to reduce energy expenditure for thermal regulation, ultimately influencing survival. Although this phenomenon may occur for some high-altitude breeders, many banded dippers in our study area consistently wintered on the river even though their breeding site was only a few hundred meters upstream on the creeks and not significantly higher in elevation.

An alternative explanation for the dipper's altitudinal migration is that birds adaptively respond to changes in hydrograph patterns that can alter food availability. During fall and winter, when water levels are low, seasonal increases in food supply on the main river could conceivably drive the downstream migration. Large salmon and steelhead runs occur throughout the fall and winter along the Chilliwack River with escapement records of over 500 000 salmon in 1999 (British Columbia Fisheries, unpubl. data). Throughout the winter, we routinely observed dippers feeding on salmon eggs in addition to invertebrates in shallow pools. Other large salmon-bearing rivers throughout south-coastal British Columbia also support high winter densities of American Dippers (CAM, pers. obs.). The return to the smaller, high-elevation tributaries in spring during peak snowmelt may be a response to marked increases in discharge, which cause turbulence and carry high sediment loads that can reduce prey abundance and prey availability on the larger rivers. Although migration is energetically costly, this strategy may be advantageous to dippers if it maximizes food availability through hydrological stability and if it lowers energy expenditure required for thermoregulation.

DIPPERS AS BIOLOGICAL INDICATORS

The presence of two distinct migratory groups within a single population has implications for using dippers as indicators of habitat quality or stream condition, since exposure to environmental stressors may differ between migrants and residents. Migrants use a larger area during the course of a year than residents. In watersheds where a source of pollution affects a single tributary and the area downstream, differences in habitat use during the annual cycle can result in significant variation in observed contaminant levels among individual dippers (Morrissey et al. 2004). In addition, resident dippers that remain on their territories year-round have the advantage of being familiar with good feeding and roosting sites in winter, possibly with improved fitness consequences. Resident dippers also initiate breeding earlier than migrants, which has a positive effect on their seasonal productivity (Morrissey 2004). If reproduction or survival are used as measures of environmental quality, knowledge about the differences in migratory patterns are necessary to correctly assess the effects of habitat degradation.

Similar to many wintering waterfowl species, the majority of the dipper population within a watershed appears to concentrate during the fall and winter months. We found some disparity between the ratio method and the Jolly-Seber model in estimating population size, especially for 1999. Confidence intervals overlapped for both 2000 and 2001, but it is unclear which method was more accurate. Using similar census methods, D'Amico and Hemery (2003) estimated that the probability of detecting Eurasian Dippers during the breeding season was high (0.63–0.94) and consistent across years. However, they used a binomial model to estimate population size which closely matched territory mapping estimates. If abundance is used as a measure of stream quality, one must be cognizant of the timing of censuses to report changes in density as a result of site quality rather than those caused by annual migratory movements. Furthermore, it is important to take into account whether the survey area consists of breeding or wintering habitat, as this will also strongly influence census numbers. We recommend that future studies of American Dippers consider the natural fluctuations in population density and distribution within a watershed during the annual cycle, as these may be critical for assessing exposure to and effects from a variety of environmental stressors.

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