

## LIFE HISTORY CORRELATES OF ALTERNATIVE MIGRATORY STRATEGIES IN AMERICAN DIPPERS

ELIZABETH A. GILLIS,<sup>1</sup> DAVID J. GREEN, HOLLY A. MIDDLETON, AND CHRISTY A. MORRISSEY

*Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6 Canada*

**Abstract.** Partial migration is thought to be a critical step in the evolution of avian migration, but data on the life history correlates of alternative migratory strategies are extremely limited. We have studied a partially migratory population of American Dippers since 1999. This population is composed of sedentary individuals (residents) that maintain the same territory year round and altitudinal migrants that share winter grounds with residents, but move to higher elevations to breed. We used seven years of data on individually marked birds to (1) determine if individuals consistently use the same migratory strategy, (2) determine if offspring have the same strategy as their parents, and (3) estimate reproductive and survival rates of the two migratory strategies. We evaluate hypotheses for the persistence of partial migration and discuss their implication for the evolution of migration in sedentary populations. Individual American Dippers rarely switched migratory strategy (4/169 monitored more than one year). An individual's strategy, however, was not always that of its parents, indicating that, while migratory behavior may have a genetic component, environmental or social conditions probably influence the migratory strategy that an individual adopts. Sedentary dippers consistently had higher annual productivity (~1.4 more fledglings/year) than migratory dippers, but mark–recapture models suggested that migratory dippers may have slightly higher survival than residents (~3.4%). Migrants were estimated to have lower lifetime reproductive success than residents because their higher survival was insufficient to offset their lower productivity. Our data suggest that alternative migratory strategies in American Dippers are unlikely to be a fixed genetic dimorphism that persists because the two strategies have equal fitness, or because the relative fitness of the two strategies fluctuates over time. Migratory strategies in American Dippers are more likely to be condition dependent, and the two strategies persist because migrants “make the best of a bad job” by moving to higher elevations to breed. Because migrants obtained no fitness benefits by moving to seasonal breeding territories, our data are consistent with the hypothesis that migration could evolve in sedentary populations if competition for limited resources forces some individuals to seek breeding opportunities outside their initial range.

**Key words:** *altitudinal migrant; American Dipper; British Columbia, Canada; Cinclus mexicanus; cost of reproduction; partial migration; reproductive success; sedentary bird populations; survival.*

### INTRODUCTION

Avian migration has been the focus of considerable research attention over the last 50 years (Greenberg and Marra 2005). Although debate over the processes leading to the evolution of old and new world migration systems continues, many authors argue that tropical–temperate migrants evolved from sedentary tropical ancestors (Rappole 1995, Safriel 1995, Berthold 1999, Bell 2000; but see also Salewski and Bruderer 2007). The principal support for the tropical ancestor hypothesis is that the majority of long-distance migrants to North America, Europe, and the temperate regions of Asia

have sedentary conspecifics or congeners that breed in the Neotropics, African, or Asian Tropics, respectively (Rappole and Jones 2002).

Two scenarios have been proposed to explain how migratory behavior could initially appear in a sedentary ancestral population. One suggests that migratory behavior evolves because some individuals obtain fitness benefits by dispersing into seasonal breeding habitat outside the geographical range of the sedentary population (Cox 1968, 1985, Rappole 1995, Chesser and Levey 1998). The other argues that rather than dispersing “voluntarily,” less competitive individuals are forced to move outside the original range because of intense competition for limited breeding territories (Cox 1968, 1985). These scenarios are not mutually exclusive; either one will result in a partially migratory population, in this case a population comprising sedentary and migratory individuals that share a winter range.

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<sup>1</sup> Present address: Resource Management and Officer Technology Department, Malaspina University-College, 900 Fifth Street, Nanaimo, BC V9R 5S5 Canada. E-mail: gillisl@mala.bc.ca

Partial migration is regarded as the turntable upon which selection can act to produce completely migratory or sedentary species (Berthold 1999, Bell 2000), yet exclusively migratory or sedentary birds are relatively rare (Dowsett 1988, Levey and Stiles 1992, Chan 2001). This raises the question of how both migratory and sedentary strategies are maintained. If the alternative strategies are a fixed genetic dimorphism, they could persist if the two strategies have equal fitness (Gauthreaux 1982, Lundberg 1987, 1988). In this case, reproductive rates of migrants and residents can differ, but any difference in reproductive success must be offset by differences in survival (Cox 1968, 1985, Greenberg 1980). A fixed genetic dimorphism could also persist in a population if temporal fluctuations in which strategy was "best" were to cause fluctuations in the direction of selection (Lundberg 1987, 1988).

Migratory and sedentary strategies also can both persist if the strategies, rather than being fixed genetic traits of individuals, are condition dependent and vary with environmental circumstances (Chan 2005) or attributes of the individual (e.g., sex, age, dominance; Ketterson and Nolan 1983, Lundberg 1987, Gauthreaux 1993). Individual behavior may then change over time, and the behavior of offspring may differ from that of their parents. In species where individuals are known to switch strategies, residents typically appear to have higher reproductive success than migrants (Harper 1985, Warriner et al. 1986, Adriaensen and Dhondt 1990, Warkentin et al. 1990, Morrissey 2004) and individuals are more likely to switch from being migratory to being sedentary than the reverse (Adriaensen and Dhondt 1990). Migrants may therefore be less competitive individuals that are simply "making the best of a bad job" (Lundberg 1987, 1988, Adriaensen and Dhondt 1990).

To date, attempts to evaluate hypotheses for the evolution and maintenance of partial migration have been limited by the paucity of long-term studies that monitor the behavior, productivity, and survival of individuals and that can calculate the relative costs and benefits of the two migratory strategies. In this paper we use data from a long-term study of migratory and sedentary American Dippers (*Cinclus mexicanus* Swainson) in British Columbia, Canada, to determine if individuals consistently use the same migratory strategy, if offspring have the same strategy as their parents, and to estimate the reproductive and survival rates associated with the two strategies. We subsequently use these data to evaluate hypotheses for the persistence of partial migration and discuss the implication of our results for the evolution of migration in sedentary populations.

## METHODS

### *Study system*

American Dippers are aquatic passerines dependent on fast-flowing mountain streams for food and nesting habitat. Dippers feed primarily on aquatic insect larvae

and small fish, and place their nests 2–3 m above fast-flowing water on cliff ledges, boulders, ends of overhanging logs, undercut banks with exposed tree roots, and bridges (Price and Bock 1983, Morrissey 2004). Across most of their range, American Dippers are sedentary and occupy permanent territories year round (Kingery 1996). In mountainous areas, however, up to 90% of individuals are migratory (Price and Bock 1983, Morrissey et al. 2004). These migratory individuals move between low-elevation wintering areas, which they share with year-round residents, and higher elevation breeding areas. Thus American Dippers differ from "classical" partial migrants (*sensu* Lack [1944] cited in Terrill and Able [1988]) in that migratory and sedentary individuals share wintering, rather than breeding, grounds.

We have been studying a population of American Dippers in the Chilliwack River watershed (49°0' N, 121°4' W), located ~100 km east of Vancouver in southwestern British Columbia, Canada, since 1999. The watershed ranges from 20 to 2500 m elevation and drains an area of >1200 km<sup>2</sup>. The 43.5-km Chilliwack River runs between Chilliwack Lake (640 m) and the Vedder River (40 m). Dippers were monitored throughout the year at eight sites (each 2 km long; elevation range 40–420 m) located at ~4-km intervals along the Chilliwack River (see map in Morrissey et al. [2004]). Migratory Dippers were also monitored during the breeding season on seven tributaries. Monitored tributary sections ranged in length from 1 km to 6.5 km, with maximum elevation ranging from 200 m to 1000 m. No birds overwintered at the sites on the higher elevation tributaries (Morrissey et al. 2004).

To date, we have banded over 800 individuals with unique combinations of three color bands and a metal USFWS band. Of these birds, 48% were banded as 10–14 day-old nestlings, with the remainder banded as adults. Breeding adults were sexed based on the presence of a brood patch and behavior (only female American Dippers incubate eggs and brood young; Kingery 1996). Since 2003, nestlings have been sexed using a DNA-based test that relies on PCR amplification of a section of the CHD1 genes (CHD1-W and CHD1-Z) located on the avian sex chromosomes (see Griffiths et al. [1998] for details of the method). Sexes of the nestlings banded before 2003 and nonbreeding adults are unknown.

We classified American Dippers as either year-round residents (residents) or altitudinal migrants (migrants). Residents occupy multipurpose territories on the main stem of the river year round and were never observed >1 km from their territory. Migrants were identified in one of two ways: (1) they wintered on the Chilliwack River and left in the spring to take up breeding territories elsewhere, or (2) they bred on tributaries at least 2 km upstream from the river confluence and left these territories after the breeding season to winter either on the main stem of the river or in another watershed. On average, migrants travel 5.8 km (range 2–20.8 km),

gaining an average of 226 m (range 10–735 m) as they move to higher elevation territories in the breeding season ( $n = 33$  birds, D. J. Green, *unpublished data*). The migratory strategy of birds that were resighted fewer than two times after banding or that disappeared midway through the winter was uncertain and these birds were excluded from the analyses.

Resident American Dippers strongly defend their territory during the breeding season, excluding conspecifics. Territory boundaries are less well defined in the winter, with the resident pairs defending some portions of their territories but tolerating conspecifics in others. Like residents, migrants strongly defend their breeding territory. Unlike residents, migratory pairs do not overwinter together; individual migrants move to wintering territories that can overlap with the territories of residents or migrants. Individual migrants are nevertheless observed to defend parts of their wintering territory (I. Whitehorne, *unpublished data*). Residents and migrants are both known to exhibit high levels of fidelity to both breeding and wintering territories (Morrissey et al. 2004, Middleton et al. 2006).

#### *Monitoring reproductive success and breeding performance*

We monitored breeding birds at river and higher elevation creek sites from the start of the breeding season (March) until completion of the final nesting attempt (July) in 1999–2001 and 2003–2006. Over the seven breeding seasons, we monitored 297 nesting attempts by 192 pairs of birds. These pairings included 166 different females. On average, 22 resident and seven migratory pairs were monitored in any given year. Results for the years 1999–2001 have previously been published (Morrissey 2004) but we include data from these years to evaluate yearly variation in breeding performance of residents and migrants and to permit concurrent evaluation of survival and reproduction.

We located nests by walking sections of river or creek and following birds while they were nest-building, incubating, or provisioning nestlings (see Plate 1). Dates of clutch initiation, incubation, and hatching were typically known to within 1 day or were back-calculated assuming that one egg was laid per day, the incubation period was 16 days and the nestling period was 25 days (Price and Bock 1983, Kingery 1996). If nests were accessible, clutch size was determined after laying was complete, i.e., when no additional eggs had been laid for 2 days. Brood size was determined for nests with at least one chick during routine banding when nestlings were 10–14 days old. Breeding attempts were considered successful if at least one fledged young was observed. Because newly fledged American Dippers are difficult to locate, we assumed that the total number of fledglings from successful nests was equal to the brood size at banding. This assumption is supported by data from a subset of nests monitored intensively from banding through fledging.

Differences in the breeding performance of residents and migrants across years were evaluated by comparing (1) dates when females laid the first egg of the season, (2 and 3) clutch and brood sizes of the first nesting attempt, (4) the success of first nesting attempts, (5 and 6) the likelihood of initiating second clutches following the success or failure of the first, (7) the probabilities of fledging at least one offspring, and (8) the total numbers of offspring fledged per year. Because 29% of females were monitored in more than one year of the study, we included female identity as a random factor in all analyses. We used a REML or GLMM procedure in Genstat 9.1 (2006) for Windows (VSN International, Hemel Hempstead, UK) to analyze continuous and categorical variables, respectively. In all analyses we initially fitted a full model with all explanatory variables and their interaction terms. A final model was selected by progressively eliminating nonsignificant ( $P > 0.05$ ) terms until only significant terms remained. Significance was assessed using either the change in model deviance associated with dropping the term of interest from the model or the Wald statistic when the term of interest was the last term entered in a model. The Wald statistic approximates the chi-square distribution. Unless otherwise stated, values are reported as mean  $\pm$  SE.

#### *Population surveys and survival analysis*

We conducted censuses at the eight sites on the main river in November, January, March, May, and July each year from 1999 to 2006. Censuses were routinely conducted in the first two weeks of each month by two observers who walked along set stretches of the riverbank and searched all channels and lower reaches of creeks where they met the river at each site. During censuses, we recorded all birds observed and confirmed the band combinations of all marked birds using a 10–40 $\times$  spotting scope. Annual survival for residents and migrants was estimated for birds that overwintered on the eight study sites located on the main river. Recapture histories were based on resighting of all birds during the November or January censuses conducted from winter 1999/2000 to winter 2006/2007.

We estimated annual survival of migrants and residents using mark–recapture methods (see Lebreton et al. [1992] for a detailed review). This method allowed us to estimate survival ( $\phi$ ) while accounting for differences in the probability of detecting an individual if it was alive ( $p$ ). Thus, survival estimates are not underestimated simply because some individuals are less likely to be observed. We combined data from both sexes when estimating survival because previous studies on European Dippers (Lebreton et al. 1992, Loison et al. 2002) and analysis of our data on known-sex individuals did not detect differences in survival between males and females.

We were interested in whether survival differed with migratory strategy ( $s$ ), among years ( $y$ ), with strategy and year ( $s \times y$ ), or with neither strategy nor year ( $n$ , i.e.,

constant). We assumed that detectability ( $p$ ) could also differ between strategy, among years, with both strategy and year, or neither strategy nor year. We therefore evaluated 16 candidate models. For the survival analysis and model evaluation, we used program MARK Version 4.3 (White and Burnham 1999). We first used a simulation approach to evaluate the goodness of fit between our data and our global model ( $\phi(s \times y) p(s \times y)$ ). We generated a distribution of expected deviances from 1000 random simulations of the recapture histories of our American Dippers and compared the observed to simulated deviance. Our data adequately fit the global model ( $\phi(s \times y) p(s \times y)$ ;  $P = 0.60$ ). We then estimated  $\hat{c}$  (the variance inflation factor) by dividing the observed deviance by the mean deviance from the simulations. The variance inflation factor was very low ( $\hat{c} = 1$ ) indicating that the data were not overdispersed. We therefore did not need to correct the AIC values for overdispersion of the data (Burnham and Anderson 2002).

We used program MARK to estimate survival and model deviance for each of the 16 candidate models using the logit-link function. The relative fit of each model was evaluated using the quasi-Akaike's information criterion (QAIC<sub>c</sub>) in which the AIC value was corrected for small sample size. The survival estimates we present are the result of averaging the survival estimates of models whose  $\Delta\text{QAIC}_c < 4$ . The model-averaging procedure is similar to calculating a weighted average, but in this case, the survival estimates are weighted by the normalized QAIC<sub>c</sub> weights as opposed to sample size (Burnham and Anderson 2002). We chose  $\Delta\text{QAIC}_c < 4$  as our cutoff value because models with  $\Delta\text{QAIC}_c < 2$  are all substantially supported by the data, whereas models with  $\Delta\text{QAIC}_c$  values of 4–7 have considerably less support (Burnham and Anderson 2002).

#### *Estimating reproductive value of residents and migrants*

We calculated the predicted lifetime reproductive value of resident and migrants as

$$\text{reproductive value} = b_s + \sum_{t=2}^7 l_t \times b_s$$

where  $b_s$  is the strategy-specific annual productivity of residents and migrants;  $l_t$  is the probability of surviving to age  $t$  based on annual survival estimates (where  $S_s$  is strategy-specific annual survival) of wintering American Dippers:

$$\text{annual survival} = \prod_1^t S_s.$$

When calculating the predicted lifetime reproductive value, we assumed that (1) individuals do not switch migratory strategies, (2) mortality and reproductive success are independent of age, and (3) individuals do not live more than 7 years.

## RESULTS

During the course of this study, we classified 152 banded American Dippers as being residents and 190 as migrants. Individual residents and migrants were monitored over 1–6 years. Of the 169 individuals monitored for >1 year (77 residents and 92 migrants), only four individuals altered their migratory strategy. Two males switched from being migratory to sedentary and two females switched from being sedentary to migratory.

Over the course of this study, 52 Dippers banded as nestlings recruited into the study breeding population. The migratory strategy of these recruits was not always that of their parents. Of the resident nestlings, 38% became residents while the remainder became migrants ( $n = 42$  recruits). Of the migratory nestlings, 50% became migrants while the remaining 50% became residents ( $n = 10$  recruits).

### *Reproduction*

Dippers initiated clutches between early March and mid-June (residents 6 March–13 June, migrants 18 March–20 June). Resident females began laying eggs almost two weeks earlier than migrant females (Table 1). The mean date when first clutch egg laying was initiated varied among years ( $\chi^2 = 35.8$ ,  $df = 6$ ,  $P < 0.001$ ) and differences between the mean clutch initiation dates of residents and migrants tended to vary annually (interaction  $\chi^2 = 11.2$ ,  $df = 6$ ,  $P = 0.07$ ), but the mean start date for residents was earlier than for migrants in all years (range 7–20 days earlier).

The clutch sizes in the first nests of residents and migrants did not differ significantly (Table 1) even though clutch sizes declined with later initiation dates ( $\chi^2 = 9.3$ ,  $df = 1$ ,  $P < 0.001$ , slope =  $-0.013 \pm 0.004$ ). There was little annual variation in the clutch size of first nests ( $\chi^2 = 4.1$ ,  $df = 6$ ,  $P = 0.66$ ). In contrast, brood sizes of residents were slightly higher than those of migrants (Table 1). However, this difference did not persist after controlling for seasonal declines and interannual variation in brood size (for date (season),  $\chi^2 = 9.3$ ,  $df = 1$ ,  $P < 0.001$ , slope =  $-0.026 \pm 0.007$ ; for year,  $\chi^2 = 12.4$ ,  $df = 6$ ,  $P = 0.05$ ; for migratory behavior,  $\chi^2 = 0.2$ ,  $df = 1$ ,  $P = 0.65$ ).

There was no detectable difference in the probability that residents and migrants would fledge at least one chick from their first nesting attempt of the year (Table 1). However, residents were more likely than migrants to initiate a second clutch if their first nesting attempt was successful (i.e., to double brood; Table 1). The probability a female would double brood decreased with date of first nest initiation ( $\chi^2 = 14.1$ ,  $df = 1$ ,  $P < 0.001$ ), and after controlling for initiation date, residents and migrants were equally likely to double brood ( $\chi^2 = 0.2$ ,  $df = 1$ ,  $P = 0.65$ ). If their first nesting attempt failed prior to fledging chicks, residents and migrants were equally likely to attempt a second clutch (Table 1). The probability of initiating a replacement clutch was not

TABLE 1. Breeding performance of resident and migrant American Dippers (*Cinclus mexicanus*) in the Chilliwack River watershed, British Columbia, Canada, for 1999–2001 and 2003–2006.

Performance measure	Residents	Migrants	$\chi^2_1$	<i>P</i>
Date first egg is laid†	30 Mar $\pm$ 1 d (126)	12 Apr $\pm$ 2 d (50)	35.4	<0.001
Clutch size of first nest	4.4 $\pm$ 0.1 (103)	4.2 $\pm$ 0.1 (39)	1.7	0.19
Brood size of first nest†	3.7 $\pm$ 0.1 (101)	3.3 $\pm$ 0.2 (34)	4.2	0.04
Success rate of first nest	0.69 $\pm$ 0.05 (135)	0.57 $\pm$ 0.08 (53)	2.7	0.10
Probability of laying second clutch:				
Following a failed first clutch	0.39 $\pm$ 0.09 (41)	0.33 $\pm$ 0.11 (23)	0.2	0.69
Following a successful clutch	0.49 $\pm$ 0.06 (94)	0.27 $\pm$ 0.09 (30)	4.7	0.03
Probability of fledging $\geq$ 1 offspring	0.76 $\pm$ 0.04 (111)	0.64 $\pm$ 0.08 (44)	2.5	0.11
Annual productivity	3.7 $\pm$ 0.3 (110)	2.3 $\pm$ 0.4 (42)	8.7	0.003

Note: Values reported are model predictions  $\pm$  SE (sample sizes in parentheses) derived from mixed models where female identity is included as a random term.

† Model predictions are reported after controlling for significant year effects.

influenced by the date when females initiated their first nesting attempt ( $\chi^2 = 0.6$ ,  $df = 1$ ,  $P = 0.43$ ).

No statistical difference was found between residents and migrants in the probability that they would produce at least one fledgling during a breeding season. However residents, as a result of initiating breeding earlier and being more likely to double brood, had higher annual reproductive success than migrants (Table 1). In fact, residents had higher annual productivity than migrants in every year of the study, fledging, on average, 1.4 more chicks than migrants in each breeding season (Fig. 1, Table 1; year effect:  $\chi^2 = 10.6$ ,  $df = 6$ ,  $P = 0.10$ ; year  $\times$  status interaction:  $\chi^2 = 2.7$ ,  $df = 6$ ,  $P = 0.84$ ).

#### Annual survival

Five of the 16 survival models considered were strongly supported by the resighting data collected during the November and January censuses ( $\Delta QAIC_c \leq 2$ ; Table 2). Two of these five models suggested residents had lower survival than migrants (Table 2). The three other models supported by the data, however,

did not include migratory strategy (Table 2). Model averaging, in which the survival estimates from the supported models were combined based on the weight of support for each model, suggested that annual survival of residents was 3.4% lower than that of migrants (Fig. 2), with overall mean annual survival estimates of 53.9%  $\pm$  0.8% for residents and 57.3%  $\pm$  0.9% for migrants. All of the supported models suggested that detectability of migrants was lower than that of residents; two models indicated that detectability also varied among years (Table 2; model-averaged detectability  $p = 86.7\% \pm 3.0\%$  for residents and 36.7%  $\pm 2.5\%$  for migrants).

#### Reproductive value of residents and migrants

Based on the measured annual productivity (Table 1) and survival rates (Fig. 2), resident American Dippers are expected to fledge 2.6 more chicks than migrants over the course of their lifetime (7.8 vs. 5.2 chicks per breeding female per lifetime). For residents and migrants to have equivalent reproductive values, either the annual survival of migrants would need to be  $\sim 18\%$  higher than

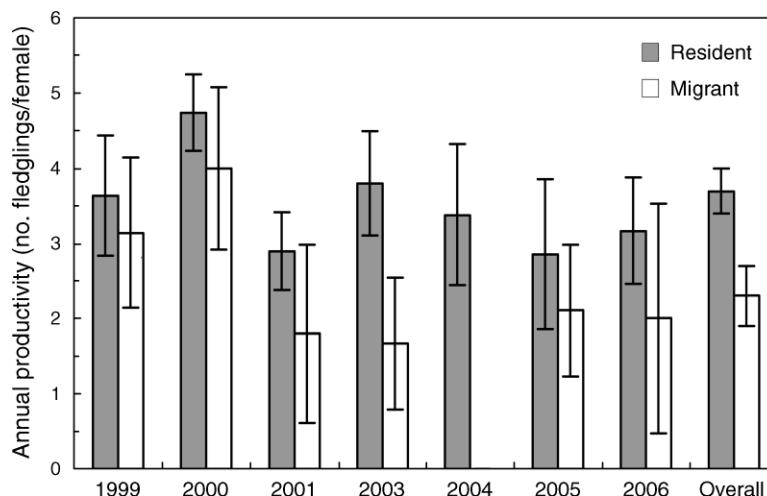


FIG. 1. Annual productivity (mean  $\pm$  SE) of breeding resident and migrant American Dippers (*Cinclus mexicanus*). The analysis used data from banded females for which we had information for the entire breeding season. Sample sizes (by year) for residents and migrants, respectively, were 11 and 7 (1999), 27 and 6 (2000), 27 and 5 (2001), 16 and 9 (2003), 8 and 3 (2004), 7 and 9 (2005), and 14 and 3 females (2006).

TABLE 2. Mark–recapture models for American Dippers that wintered in the Chilliwack watershed, southwestern British Columbia, Canada.

Model structure		Model statistics				
$\phi$	$p$	$K$	Dev.	$\Delta\text{QAIC}_c$	$w_i$	$w_1/w_i$
$n$	$s \times y$	11	77.5	0	0.274	...
$s$	$s \times y$	12	76.1	0.7	0.194	1.4
$s$	$s$	4	93.2	0.8	0.182	1.5
$n$	$s$	3	83.5	0.8	0.182	1.5
$y$	$s$	9	68.2	1.65	0.121	2.3

Notes: Parameters included in the survival ( $\phi$ ) and detectability ( $p$ ) portions of the model are:  $s$ , migratory strategy (sedentary or migratory);  $y$ , year;  $s \times y$ , strategy and year interaction; and  $n$ , neither strategy nor time. Of the 16 models evaluated, only those models with good support (Akaike weight,  $w_i > 0.1$ ) are included in the table.  $K$  is the number of parameters in the model, Dev. is the model deviation, and  $\Delta\text{QAIC}_c$  is the difference between the  $\text{QAIC}_c$  value of the model and the model with the lowest  $\text{QAIC}_c$  value. The likelihood of the model relative to the other models considered is  $w_i$ , which can be interpreted as the relative probability of the model given the data. The evidence ratio ( $w_1/w_i$ , where  $w_1 = w_i$  of the best supported model) is the relative likelihood of the model compared to the most parsimonious model.

that of residents (given the measured annual productivity differences) or annual productivity of residents would need to be no more than 0.3 fledgling per year higher than productivity of migrants (given the measured annual survival differences).

#### DISCUSSION

We monitored the migratory behavior, productivity, and survival of migratory and sedentary American Dippers breeding in the Chilliwack River Valley, British Columbia, Canada over seven years. We found that individual Dippers consistently used the same migratory strategy. Migratory individuals consistently had lower productivity ( $\sim 1.4$  fledglings per year) than residents, primarily because migrants initiate breeding later than residents and are less likely to double brood, as shown in this study and by Morrissey (2004). However, mark–recapture models suggested that migrants had slightly ( $\sim 3.4\%$ ) higher annual survival than residents. Never-

theless, our calculations suggest that the higher survival of migrants is insufficient to offset their lower productivity; migrants will, on average, have lower lifetime reproductive success than residents.

The trade-off between productivity and survival observed in this study may arise because of a direct cost associated with reproduction (Nur 1984, Golet et al. 1998, Hanssen et al. 2005), or an indirect cost associated with maintaining a permanent, multipurpose territory all year. The defense of a permanent territory may reduce survival by imposing a direct energetic cost (Powers and McKee 1994), or by constraining the ability of residents to use safe refuges or track winter resources (Pérez-Tris and Tellería 2002, Tellería and Pérez-Tris 2004). The latter is supported by the lower resighting probability for migrants (37% vs. 87%), which suggests that migrants may make more temporary excursions from the monitored wintering sites. We are currently examining whether migrants have higher survival because they are more adept at finding refuges from winter floods, or whether they have winter territories with greater food abundance.

#### *What explains the persistence of both migratory and sedentary strategies?*

In American Dippers living in mountainous areas, many wintering populations are composed of migratory and sedentary individuals (Price and Bock 1983, Kingery 1996, Morrissey 2004). Where partial migration occurs, both strategies are documented in all years (Price and Bock 1983, this study), indicating that the two strategies can coexist for many years in multiple locations. Migratory and sedentary strategies could persist as a fixed genetic dimorphism, with the two strategies having equal fitness payoffs (i.e., in an evolutionary stable state), or because temporal fluctuations in which strategy is “best” cause fluctuations in the direction of selection. Alternatively, migratory strategy could be a condition-dependent trait and individuals might switch their strategy depending on environmental or social conditions (for example, if competitive asymmetries between individuals change with time;

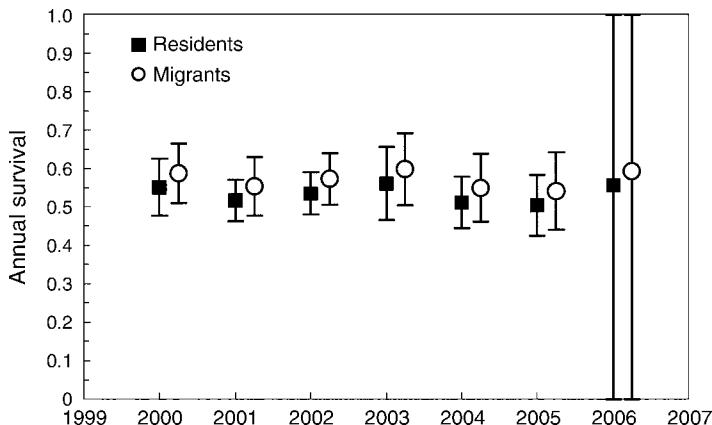


FIG. 2. Annual survival estimates (mean  $\pm$  SE) of resident and migrant American Dippers in the Chilliwack watershed, British Columbia, Canada. Annual survival was measured from one winter to the next (e.g., 2000 survival was survival from winter 1999/2000 to winter 2000/2001). Survival was estimated using mark–recapture methods for sighting data collected on 91 resident and 93 migrant wintering individuals. Survival estimates for 2006 have high standard errors because detectability, which is used in calculating survival, is based on only one year of resighting data for birds first marked in 2006.



PLATE 1. Adult American Dipper with moss, a common nesting material. Nests were located by following birds while they were nest-building. Once located, nests were monitored throughout the breeding season to measure reproductive success and breeding performance. Photo credit: Roberta Olenick, Never Spook the Animals Wildlife Photography, Vancouver, British Columbia.

Ketterson and Nolan 1983, Lundberg 1987, 1988, Gauthreaux 1993, Kaitala et al. 1993). If migratory strategy depends on condition, both strategies could persist even if fitness payoffs differ, if less competitive individuals make “the best of a bad job” by adopting the less successful strategy (Adriaensen and Dhondt 1990).

In our population of American Dippers, migratory and sedentary strategies appear unlikely to persist as a fixed genetic dimorphism with equal fitness payoffs. Resident Dippers had higher annual productivity than migrants in every year of this study, and differences in survival were never large enough to balance the differences in productivity. Residents are predicted to produce 33% more fledglings than migrants over the course of their lifetime (7.8 vs. 5.2 fledglings per female). Similarly, Adriaensen and Dhondt (1990) showed that sedentary male European Robins (*Erithacus rubecula*) had higher lifetime reproductive success than their migratory counterparts, although in that study migrants and residents shared a breeding rather than wintering ground. In contrast, Herzog and Keppie (1980) suggest that sedentary and migratory Spruce Grouse (*Falcipennis canadensis*) that share a wintering ground obtain

equal payoffs from each strategy, although the percentage of females with broods rather than the number of young fledged was used a measure of fitness in their study.

Annual variation in breeding performance of American Dippers may reduce differences in the payoffs to each strategy, but we found no evidence that it altered which strategy was superior. Residents had higher productivity in all years (Fig. 1). In only one year (1999) was the breeding performance of migrants similar enough to that of residents that the higher survival experienced by migrants would have resulted in similar fitness payoffs to the two strategies. This suggests that alternative migratory strategies in American Dippers are not a fixed genetic dimorphism that persists as a result of fluctuating selection, at least on the comparatively short time scale studied here.

Initially, our data appear to suggest that migratory strategies in American Dippers are unlikely to be condition dependent because individuals are rarely observed to switch strategies. Migrants would be expected to become sedentary in order to gain the higher fitness payoffs associated with this strategy.

However, the failure to observe changes in individual behavior does not preclude migration from being a condition-dependent trait. For example, individuals would not be expected to switch strategies if their competitive ability does not change over time or the benefits of breeding site philopatry outweigh the potential gains obtained by switching strategy (Kaitala et al. 1993, Middleton et al. 2006).

Given that our data suggest that alternative migratory strategies would not persist as a fixed genetic dimorphism, and because offspring frequently adopt a migratory strategy that differs from that of their parents, we believe that, although the predisposition to migrate may have a genetic basis (Adriaensen and Dhondt 1990, Berthold 2001), migration in American Dippers is a condition-dependent trait. If this is the case, the two strategies probably persist despite having unequal fitness payoffs because less competitive individuals make "the best of a bad job" by becoming migrants. In the case of American Dippers, suitable nest sites are often limiting (Price and Brock 1983), and less competitive individuals may be forced to either move to higher elevation creeks to find suitable nesting habitat or forgo a breeding season. Because the annual survival of American Dippers is relatively low (40–60%), as shown by this study and by Price and Brock (1983), selection is likely to favor individuals that migrate and have some reproductive success over individuals that remain sedentary and do not breed for one or more years (Pianka 1976). Once individuals adopt a migratory strategy, they may rarely switch, for reasons previously discussed.

Our conclusions are based on the assumption that permanent emigration of residents and migrants is equal and survival estimates are therefore unbiased. We believe this assumption to be true because residents and migrants are highly philopatric to both breeding and wintering territories (Morrissey et al. 2004, Middleton et al. 2006). In addition, we monitor eight wintering sites spread over ~40 km, and no individuals of either strategy have permanently moved between sites, suggesting that emigration rates of both migrants and residents are low. If, however, migrants do have higher permanent emigration rates than residents, the survival advantage of migrants will be underestimated. This would not alter our conclusion that the alternative strategies do not have equal fitness payoffs and are therefore unlikely to persist as a genetic dimorphism unless permanent emigration rates for migrants are 14.6% higher than for residents.

*Possible implications for the evolution of migration in sedentary bird populations*

Many models for the evolution of avian migration argue that ancestral species were typically sedentary and that an early step in the evolution of long-distance temperate–tropical migration systems was partially migratory populations, composed of sedentary and

migratory individuals that overwinter together but breed in separate areas (Rappole 1995, Safriel 1995, Berthold 1999, Bell 2000). Migratory behavior could arise because some individuals are either forced to breed outside their traditional range or obtain fitness benefits from migrating to breed in seasonal habitat where resources are plentiful and competition is initially low (Cox 1968, 1985, Rappole 1995, Chesser and Levey 1998). American Dippers are a good model in which to evaluate these alternatives because migrants overwinter with sedentary individuals, but move to higher elevations to breed. We found that migrants obtained no reproductive benefits from leaving their wintering grounds, suggesting that, at least for American Dippers, competition for limiting breeding resources may be the selective force that causes some individuals to move to higher elevation streams in search of breeding opportunities. For this species, the limiting breeding resource is most likely nesting sites (Price and Bock 1983).

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