Altitudinal migration in American Dippers (*Cinclus mexicanus*): Do migrants produce higher quality offspring?

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Abstract: Breeding at high elevations can favour life-history strategies in which parents shift to investing in higher quality rather than higher numbers of offspring. In American Dippers (*Cinclus mexicanus* Swainson, 1827), altitudinal migrants produce fewer fledglings than sedentary individuals (residents) that breed at lower elevations. We examined whether migrants compensate for their lower fecundity by providing their offspring with a higher quality diet and (or) more food, and producing higher quality offspring. Nestling diet was assessed using observations and stable isotope analysis of feathers grown during the nestling period. Nestling quality was assessed using a condition index (residuals from a mass–tarsus regression) and postfledging survival. We found that migrants fed their offspring less fish, and despite having higher feeding rates, had lower energetic provisioning rates than residents. Migrants also produced offspring that were in worse condition and had lower postfledging survival. This study found no evidence that altitudinal migration is associated with a trade-off favouring the production of smaller numbers of higher quality young. Instead our data provide support for the hypothesis that altitudinal migration in American Dippers is an outcome of competition for limited nest sites at lower elevations that forces some individuals to move to higher elevations to breed.

Résumé : La reproduction aux hautes altitudes peut favoriser des stratégies démographiques dans lesquelles les parents investissent dans des rejetons de plus grande qualité plutôt que dans un nombre plus élevé de rejetons. Chez le cincle d'Amérique (*Cinclus mexicanus* Swainson, 1827), les individus qui migrent en altitude produisent moins de petits à l'envol que les individus sédentaires (résidants) des altitudes plus basses. Nous vérifions si les migrateurs compensent leur fécondité réduite en procurant à leurs rejetons un meilleur régime alimentaire ou un régime plus abondant et en produisant ainsi des petits de meilleure qualité. Le régime alimentaire des petits au nid a pu être déterminé par observation directe et par analyse des isotopes stables dans les plumes élaborées durant la période au nid. La qualité des petits au nid a été mesurée par un indice de condition (résidus de la régression de la masse sur le tarse) et par la survie après l'envol. Les migrateurs apportent moins de poissons à leurs rejetons et, malgré des taux d'alimentation plus élevés, ils ont des taux d'approvisionnement en énergie inférieurs à ceux des résidants. Les migrateurs produisent aussi des petits en moins bonne condition dont la survie après l'envol est inférieure. Notre étude n'offre aucune indication que la migration en altitude comporte un compromis favorisant la production de petits moins nombreux mais de meilleure qualité. Au contraire, nos données appuient l'hypothèse selon laquelle la migration en altitude chez les cincles d'Amérique résulte de la compétition pour un nombre limité de sites de nidification aux altitudes inférieures, ce qui oblige certains individus à se déplacer vers les altitudes supérieures pour leur reproduction.

[Traduit par la Rédaction]

Introduction

Altitudinal migration is a common strategy of birds occupying mountainous habitat but has been studied less intensively than latitudinal migration (Berthold 2001; Newton 2008). For most altitudinal migrants seasonal movements are relatively short and involve migrating uphill to breeding areas and downhill to nonbreeding areas (Burgess and Mlingwa 2000; Dingle 2004; Johnson and Maclean 1994; Stiles 1983). Altitudinal migration may be advantageous because it allows migrants to exploit temporal or spatial variation in food resources (Loiselle and Blake 1991; Solórzano et al. 2000), minimize the risk of nest predation (Boyle 2008; Fretwell 1980), or escape extreme climatic conditions that impact physiological function (Cox 1985).

Seasonal movements to higher elevation breeding sites can impose selection pressures that lead to elevation-specific life-history strategies. For example, a comparison of phylogeneti-

cally paired avian taxa from low- and high-elevation sites indicates that high-elevation species have smaller clutches and fewer broods per year than their low-elevation counterparts (Badyaev and Ghalambor 2001). Badyaev and Ghalambor (2001) found that the reduced fecundity in these high-elevation species is associated with increased parental care and a shift away from investment in offspring number toward investment in offspring quality. Similar life-history trade-offs have been described within species that breed on a steep-elevation gradient. For example, Dark-eyed Juncos (*Junco hyemalis* (L., 1758)) that breed at high elevations initiate breeding later and have a more compressed breeding season than Dark-eyed Juncos breeding at low elevations, and consequently produce fewer broods and fledglings per season. However, Dark-eyed Juncos at high elevations produce heavier offspring with greater fat reserves than Dark-eyed Juncos at low elevations (Bears et al. 2009).

Most populations of American Dippers (*Cinclus mexicanus* Swainson, 1827) contain altitudinal migrants, individuals that move between winter habitat on the coast or on rivers at low elevations and breeding habitat on higher elevation streams (Morrissey et al. 2004*a*; Price and Bock 1983; Willson and Hocker 2008). Some populations contain both migratory and sedentary individuals, allowing the life-history consequences of altitudinal migration to be compared in a single population. In British Columbia, Canada, migrants consistently have lower productivity than residents because they initiate breeding later and are consequently less likely to raise a second brood (Gillis et al. 2008; Morrissey 2004). Migrants, however, have higher annual adult survival than residents (Gillis et al. 2008). Gillis et al. (2008) argued that migrants were making the "best of a bad job" when moving to higher elevation breeding habitat, as the difference in adult survival was not sufficient to offset the lower productivity and the lifetime reproductive success of migrants was predicted to be lower than that of residents. This argument, however, ignores the possibility that migrants in addition to having higher annual survival as adults may also compensate for their reduced fecundity by producing offspring of higher quality.

In this paper we assess whether breeding at higher elevations can lead to a shift in the life-history strategies of American Dippers favouring the production of higher quality rather than higher numbers of offspring. We assess whether the seasonal movement of migrants enables them to exploit different prey and (or) provision at a higher rate than residents using a combination of feeding observations, estimates of energetic provisioning rates, and stable isotope analysis of juvenile feathers grown during the nestling period. Aquatic larval invertebrates are the principal prey fed to nestling dippers, but small fish are an alternative prey with higher energetic content and nutritional value (Obermeyer et al. 2006). We also examine whether differences in diet quality or provisioning rate allow migratory dippers to compensate for their lower annual fecundity by producing offspring that are in better condition and (or) have higher postfledging survival.

Materials and methods

Study species and site

American dippers are aquatic passerines that feed on freshwater invertebrates and small fish in fast-flowing rivers and mountain streams. Dippers construct large domed nests 1–5 m above the water on cliff ledges, boulders, the ends of overhanging logs, in undercut banks, and on bridges (Kingery 1996). Although both sexes contribute to territory defence, nest building, and the care of nestlings and fledglings, only females incubate eggs and brood young. Dippers will typically renest if a clutch or brood is lost early in the breeding season and may raise up to two broods per season (Gillis et al. 2008; Kingery 1996; Price and Bock 1983).

We have studied an individually marked population of American Dippers in the Chilliwack River watershed, located in the Cascade Mountain Range of southwestern British Columbia, Canada, from 1999 to 2009. This population is composed of both altitudinal migrants and sedentary individuals (residents); approximately 85% of individuals are altitudinal migrants (Morrissey et al. 2004*a*). Adults rarely switch from being migratory to sedentary or vice versa, but individuals frequently adopt a different strategy to their parents (Gillis et al. 2008). Migrants overwinter with residents on the main stem of the Chilliwack River but move to higher elevation breeding sites on first- to third-order streams in the spring (February–April). On average, migrants travel 6 km (range 2–21 km) and gain a mean 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). Migrants have lower productivity (2.3 vs. 3.7 fledglings/year) but have higher annual survival (57.3% vs. 53.9%) than residents (Gillis et al. 2008).

Monitoring reproduction and estimating nestling condition

Breeding pairs were located by searching accessible sections of the river and higher elevation creeks on foot, checking suitable locations for nests, and following any dippers seen or heard. Breeding pairs were classed as sedentary if they occupied breeding territories on or within 1 km of the main stem of the Chilliwack River and were observed in the same area during fall and winter. Pairs were classified as migrants if they occupied breeding territories on creeks more than 1 km from the main stem of the river and were not observed on these territories in winter. Where possible nests were checked every 3–7 days to determine clutch initiation dates, hatch dates, clutch and brood sizes, and the fate of all nesting attempts. Precise hatch dates were calculated using the nestling age at the first nest check after hatching. Brood size and the mean nestling condition index for each brood were determined when nestlings were banded, weighed, and measured 10–15 days (12.4 ± 2.0 days; mean ± SD) after hatching. The condition index for each nestling was estimated using the residual from a tarsus length – body mass regression. We were unable to estimate chick growth rates because of logistic difficulties associated with removing nestlings from nests located on cliffs or bridges over fast-flowing rivers or streams multiple times. When nests were inaccessible, hatch dates were estimated by backdating from the date the brood fledged assuming that fledging occurs 25 days after hatching (Price and Bock 1983). Brood size at these nests was assumed to equal the number of fledglings observed during thorough searches of the territory within 2 days of fledging.

Feeding observations

We conducted feeding observations at 68 nests between 2005 and 2008 (2005: $n = 7$; 2006: $n = 22$; 2007: $n = 18$; 2008: $n = 21$). Observations were conducted throughout the day and varied in length from 30 to 200 min (66 ± 34 min; mean ± SD). All nests were observed midway through the nestling period when nestlings were 8–14 days of age, and 23 nests were also observed a second time late in the nestling period when nestlings were 17–24 days of age. During observation periods we recorded when parents delivered food to the nest and the prey type and load size of each delivery. Prey items were classified as aquatic invertebrates, fish eggs, and small fish. Deliveries of aquatic invertebrates were not defined more precisely because deliveries often include multiple prey taxa and we were often unable to identify the taxa being delivered. However, load sizes were classified as being small, medium-sized, or large and were estimated in relation to the size of the bill. We subsequently grouped deliveries into seven categories (Table 1).

Prey and feather sampling

Prey and feather samples were collected so that we could (*i*) determine the mass and energetic content of the seven categories of food delivered to the nest and (*ii*) determine the stable isotope signatures of prey and feathers needed to calculate the proportion of invertebrates and fish in the diet of nestlings. We obtained larval aquatic invertebrate samples from six sites on the Chilliwack River and five sites on four higher elevation creeks in 2008 by turning over rocks and collecting all macroinvertebrates >2 mm long by hand. Each sample included plectopteran and ephemopteran nymphs and trichopteran larvae, all of which are preyed on by dippers (Bakus 1959; Mitchell 1968). Samples of salmonid fry were collected from the Chilliwack River and three creeks using a dip net. We targeted fish of the size observed during provisioning observations (~40 mm long). All fish sampled were either coho salmon (*Oncorhynchus kisutch* (Walbaum, 1792)) or steelhead (*Oncorhynchus mykiss* (Walbaum, 1792)). Invertebrate and fish samples were stored in ethanol prior to being transferred to the laboratory.

We calculated the energetic value of small, medium-sized, and large invertebrate deliveries by preparing 11 prey subsamples representative of each load size, determining their dry mass, and converting these mass to energetic values using published values for aquatic invertebrates (Table 1). Invertebrate subsamples contained multiple prey with individuals from each major taxa being combined to create load sizes that approximated invertebrate deliveries made by dippers, using tweezers with marks corresponding to 1/4, 1/2, and 1 dipper bill length as a reference. Invertebrate subsamples were rinsed with deionized water and oven dried at 40 °C for approximately 48 h prior to weighing. We estimated the energetic content of fish or steelhead eggs delivered to nestlings using published data on the size–mass relationship and energetic content for juvenile salmon or salmonid eggs (Table 1). Fish fed to nestlings were approximately twice the bill length of an adult dipper, so fish were assumed to be 44 mm long. Energetic values for the different prey types and load sizes were then used to calculate the energetic provisioning rate (kJ/h) during each provisioning observation.

We also prepared invertebrate and fish samples for stable isotope analysis. Invertebrate samples, which were a composite of prey collected at each site, were rinsed with deionized water and oven dried at 40 °C for 48 h. Fish samples were rinsed with deionized water and freeze-dried for 48 h. Each fish and invertebrate sample was then ground into homogenous powder and subsamples of approximately 1 mg from each fish or invertebrate sample were measured into miniature tin capsules (Costech Analytical Technologies, Inc., Valencia, California, USA) for isotopic analysis.

We collected feather samples (the innermost right primary) from a total of 63 juvenile dippers from 20 broods produced in 2008. Samples came from nestlings aged 11–14 days or recently fledged juveniles aged 25–40 days captured in mist nets set up across small channels in the natal territory. We prepared feather samples for stable isotope analysis by removing the sheath from feathers that were not completely emerged, washing all feathers in a 2:1 chloroform and methanol solution for 48 h, and air-drying them for a further 48 h. Samples of approximately 1 mg were cut from the distal tip of each feather, weighed, and transferred into miniature tin capsules for isotopic analysis.

Stable isotope analysis

Stable isotope ratios of nitrogen in the feather and prey samples were analysed at the Stable Isotope Facility, University of California Davis, Davis, California, USA, using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Sample nitrogen isotope ratios were compared with those in air. Values for ^{15}N were calculated and reported using the standard delta (δ) notation in parts per thousand (‰). During analysis, samples were interspersed with replicate laboratory standards that had been previously calibrated against NIST Standard Reference Materials (IAEA-N1, IAEA-N2, IAEA-N3, IAEA-CH7, and NBS-22). Measurement error was ±0.1‰.

Postfledging survival

We examined the postfledging survival of all banded nestlings known to have fledged between 1999 and 2008 ($n = 526$). Survival from fledging until the end of January the following year was assessed using resighting data obtained during systematic censuses of the Chilliwack River conducted five times a year between November 1999 and July 2009, detailed searches of the main stem of the river and higher elevation tributaries conducted each breeding season (2000–2009), and regular visits to the study area made to capture and mark breeding and wintering adults (for more details see Gillis et al. 2008). Our use of juvenile survival to assess the quality of offspring raised by migrants and residents could be biased if the offspring of migrants disperse farther, are more likely to disperse outside the watershed, and are less likely to be detected. However, we believe that any resighting bias is likely to be small because the offspring of migrants overwinter with the offspring of residents on the main stem of the river, the migratory strategy of an individual cannot be predicted by the strategy of their parents, and the distance from the natal territory to the point individuals are resighted is small compared with the length of the study area (Gillis et al. 2008; Middleton and Green 2008).

Table 1. Categories (defined by prey type and load size relative to bill length) used to classify prey delivered to American Dipper (*Cinclus mexicanus*) broods.

Prey delivered	Load size	Dry mass (g)	Wet mass (g)	Energetic content		
				kJ/g dry mass	kJ/g wet mass	Energetic value (kJ/delivery)
Small invertebrates	<0.25 × bill length	0.017	—	22.9*	—	0.39
Medium-sized invertebrates	0.25–0.5 × bill length	0.169	—	22.9	—	3.87
Large invertebrates	>0.5 × bill length	0.407	—	22.9	—	9.32
One fish	2 × bill length	—	1.55[†]	—	4.40[‡]	6.82
Two fish	2 × bill length	—	3.10	—	4.40	13.64
One fish and invertebrates	2 × bill length (fish) and <0.25 × bill length (invertebrates)	0.017 (invertebrates)	1.55 (fish)	22.9 (invertebrates)	4.40 (fish)	7.21 (fish and invertebrates)
Salmon egg	—	—	0.14[§]	7.8[‖]	—	1.11

Note: Representative samples were used to estimate dry mass (invertebrates) or wet mass (fish and eggs) and the energetic value associated with each type of delivery. The references give estimates for the mass and (or) energetic content of particular prey types.

*Value averaged from data reported in Brey et al. 1988 and Obermeyer et al. 2006.

[†]Value from Chingbu 2001.

[‡]Value averaged from data reported in Boldt and Haldorson 2004 and Dempson et al. 2004.

[§]Value from Rombough 1988.

[‖]Value from Hendry and Berg 1999.

Data analysis

We conducted a total of 91 provisioning observations at 68 nests containing broods produced by 54 pairs and determined the mean nestling condition of 59 broods produced by 34 pairs. We therefore used a mixed modeling approach to test whether migrants provide their offspring with a higher quality diet, deliver food at a higher rate, and produce higher quality offspring than residents. We examined five independent variables: the proportion of deliveries that contained fish, whether at least one fish was delivered during a provisioning observations (yes or no), the delivery rate of both parents (total number of feeding visits/h), the energetic provisioning rate (kJ/h), and the average nestling condition of a brood. Pair identity was included as a random term in all models. We included six explanatory variables in each model: migratory strategy, hatch date, year, brood-size category (small = 1 or 2; medium-sized = 3; large = 4 or 5), nestling age, and the time of day observations were conducted (morning 0800–1200; midday 1200–1600; afternoon 1600–2000). Brood size was categorized as a factor with three levels, as brood sizes of 1 and 5 were rare. For each analysis, we initially fitted a full model including all main effects and interaction terms, and then sequentially eliminated all nonsignificant interactions and then main effects until only significant terms remained. To ensure that the order in which terms were dropped did not influence the final model selected, we re-evaluated any term eliminated by adding and dropping it from the final reported model. We assessed the significance of terms in models by using the change in deviance or the Wald statistic associated with dropping individual terms from models. Both the change in deviance and the Wald statistic approximate a χ^2 distribution. Estimates of effects and predicted means are presented with standard errors.

We used generalized linear mixed models (GLMM) to investigate how nestling condition and the migratory strategy (altitudinal migrant or resident) of their parents influenced the postfledging survival of 526 fledglings produced by 104 pairs. Pair identity was included as a random term. Models were fitted to examine the relationship between survival and migratory strategy, survival and nestling condition, and survival and migratory strategy after controlling for nestling condition, year, and hatch date. Significance of explanatory terms was evaluated using the Wald statistic. All models were fitted using GenStat version 11 (VSN International Ltd., Hemel Hempstead, UK).

We used a two-source standard linear mixing model (Phillips 2001) and the δ^{15}N values obtained from the prey and feather samples to estimate the relative contribution fish and invertebrates make to the diet of individual nestlings. We used habitat specific δ^{15}N for the two prey types as mean isotope values differed (see Results) and a discrimination factor (fractionation value) of 2.91‰. This is the mean discrimination factor across all tissue types from 52 studies to have estimated animal–diet discrimination factors in birds (Caut et al. 2009), and matches the value (2.91‰) used in a previous study of diet composition of adult dippers (Morrissey et al. 2004b). We then compared the relative contribution fish make to the diet of nestlings provisioned by migratory and sedentary parents using a mixed model with pair (= brood) identity entered as a random term.

Results

Nestling diet

American Dippers delivered larval aquatic invertebrates, small fish, and occasionally, salmonid eggs to their broods. The proportion of deliveries that included one or more fish did not vary with the size or age of the brood (brood size: $\chi^2_{[2]}$ = 0.4, p = 0.84; age: $\chi^2_{[1]}$ = 0.6, p = 0.44). The proportion of deliveries that included fish declined across the season (date effect: –0.29 ± 0.11; $\chi^2_{[1]}$ = 6.5, p = 0.01) but did not vary with the time of day or between years (period: $\chi^2_{[2]}$ = 4.7, p = 0.10; year: $\chi^2_{[3]}$ = 1.2, p = 0.77). After controlling for seasonal variation, resident pairs fed their broods a diet that contained a greater proportion of fish than did migratory pairs ($\chi^2_{[1]}$ = 8.7, p = 0.004; Fig. 1a). This pattern remained when we analysed the diet fed to dipper broods as a binomial variable (fish: yes or no) with the duration of the focal observation entered as a covariate (GLMM; duration of observation: $\chi^2_{[1]}$ = 3.4, p = 0.07; migratory strategy: residents = 0.58 ± 0.06, migrants 0.21 ± 0.08; $\chi^2_{[1]}$ = 8.0, p = 0.006).

Larval aquatic invertebrate and fish samples collected from the river had more enriched δ^{15}N signatures than those collected from higher elevation tributaries (Table 2). Feather samples from juvenile dippers provisioned by residents on the river also had more enriched δ^{15}N signatures than feathers from juveniles provisioned by migrants on the tributaries (Table 2). The linear mixing model using habitat-specific δ^{15}N values for fish and invertebrates estimated the amount of fish in the diet of nestlings to vary from 0% to 83%. Juveniles fed by sedentary pairs had a diet containing almost three times as much fish as juveniles fed by migratory pairs (percentage (mean ± SD) of fish in diet: sedentary offspring = 32% ± 22% (n = 40); migratory offspring = 11% ± 6% (n = 23); $\chi^2_{[1]}$ = 14.9, p < 0.001).

Delivery rates

Pairs of American Dippers delivered prey to broods approximately 16 times/h (range 4–44 times/h) when nestlings were between 9 and 23 days of age. Delivery rates increased with brood size (small broods: 11.0 ± 1.9 deliveries/h; medium-sized broods: 16.5 ± 1.5; large broods: 19.5 ± 1.3; $\chi^2_{[2]}$ = 15.5, p < 0.001) but did not vary with nestling age ($\chi^2_{[1]}$ = 0.2, p = 0.68). Delivery rates also varied between years (2005: 14.9 ± 2 deliveries/h; 2006: 19.8 ± 1.4 deliveries/h; 2007: 14.2 ± 1.8 deliveries/h; 2008: 13.8 ± 1.4 deliveries/h; $\chi^2_{[3]}$ = 11.3, p = 0.01) but did not vary with the time of day or across the season (period: $\chi^2_{[2]}$ = 1.1, p = 0.59; hatch date: $\chi^2_{[1]}$ = 0.07, p = 0.79). After controlling for brood size and interannual variation, migratory pairs had a higher delivery rate than resident pairs ($\chi^2_{[1]}$ = 5.9, p = 0.02; Fig. 1b).

Energetic provisioning rate

The energetic provisioning rate to the brood, estimated in kJ/h, increased with both the parental delivery rate and the proportion of deliveries that included fish (delivery rate: $\chi^2_{[1]}$ = 29.4, p < 0.001; proportion fish: $\chi^2_{[1]}$ = 144.9, p < 0.001). Provisioning rates consequently declined across the season (date effect: –1.59 ± 0.60; $\chi^2_{[1]}$ = 7.5, p = 0.008). Pro-

visioning rates, however, did not vary significantly across years or with the time of day (year: $\chi^2_{[3]}$ = 1.8, p = 0.61; period: $\chi^2_{[2]}$ = 1.4, p = 0.50). Provisioning rates also did not increase with brood size ($\chi^2_{[2]}$ = 1.72, p = 0.43), although the trend was for provisioning rates to increase with brood size, or vary with brood age ($\chi^2_{[1]}$ = 1.6, p = 0.21). Despite the lower overall delivery rates, residents had a higher provisioning rate than migrants because a greater proportion of their deliveries included fish ($\chi^2_{[1]}$ = 7.3, p = 0.008; Fig. 1c).

Nestling quality

We were able to access and therefore calculate a mean nestling condition index for 59 of the 71 intensively monitored broods. Two factors had an effect on the mean nestling condition index of these broods. Nestlings in broods raised by residents were in better condition than nestlings in broods raised by migrants ($\chi^2_{[1]}$ = 4.0, p = 0.05; Fig. 1d). Nestlings were also in better condition in 2006 and 2007 than in 2005 and 2008 (2005: –0.56 ± 0.31; 2006: 0.24 ± 0.22; 2007: 0.22 ± 0.25; 2008: –0.48 ± 0.19; $\chi^2_{[3]}$ = 11.6, p = 0.02). Despite seasonal declines in provisioning rates, the mean nestling condition index of a brood was independent of hatch date ($\chi^2_{[1]}$ = 0.4, p = 0.84). This was not a result of seasonal declines in brood size; brood size did not vary with hatch date (date effect: –0.003 ± 0.005; $\chi^2_{[1]}$ = 0.17, p = 0.68). The mean nestling condition index of a brood also did not vary significantly with brood size ($\chi^2_{[2]}$ = 3.2, p = 0.21), although nestlings in large broods were in slightly worse condition than nestlings in small and medium-sized broods (model predictions (mean ± SE) controlling for migratory strategy and year; small broods: 0.02 ± 0.29; medium-sized broods: 0.10 ± 0.23; large broods: –0.30 ± 0.17).

Postfledging survival

Eleven percent of offspring that fledged (n = 526) between 1999 and 2008 were known to survive until the end of January following their hatch year. Fledglings produced by residents were three times as likely as fledglings produced by migrants to survive their first winter (residents: 0.12 ± 0.02; migrants: 0.04 ± 0.02; $\chi^2_{[1]}$ = 4.1, p = 0.04). The higher postfledging survival of offspring produced by residents was due, in part, to being in better condition because nestling condition had a positive effect on survival (nestling condition: $\chi^2_{[1]}$ = 8.3, p = 0.004; Fig. 2). Postfledging survival also varied between years ($\chi^2_{[8]}$ = 17.0, p = 0.03) but was not related to hatch date ($\chi^2_{[1]}$ = 1.9, p = 0.17). After controlling for nestling condition and year, postfledging survival did not vary with the migratory strategy of the parents (model predictions (mean ± SE); residents: 0.11 ± 0.01; migrants: 0.05 ± 0.03; $\chi^2_{[1]}$ = 1.7, p = 0.19).

Discussion

Breeding at higher elevations can compress the breeding season, reducing the number of clutches that can be initiated or broods that can be raised and select for investment in offspring quality rather than offspring number (Badyaev and Ghalambor 2001; Bears et al. 2009). The association between breeding elevation and productivity is observed in American

Fig. 1. Relation between migratory strategy and (*a*) the percentage of deliveries made to the nest with food that contained one or more fish, (*b*) the combined delivery rate of male and female American Dippers (*Cinclus mexicanus*) when provisioning nestlings, (*c*) the energetic provisioning rate (kJ/h), and (*d*) the mean nestling condition index of broods when banded at approximately 12 days of age. The bars show the model predictions (mean + SE) controlling for date in *a* and *c*, brood size and year in *b*, and year in *d*.
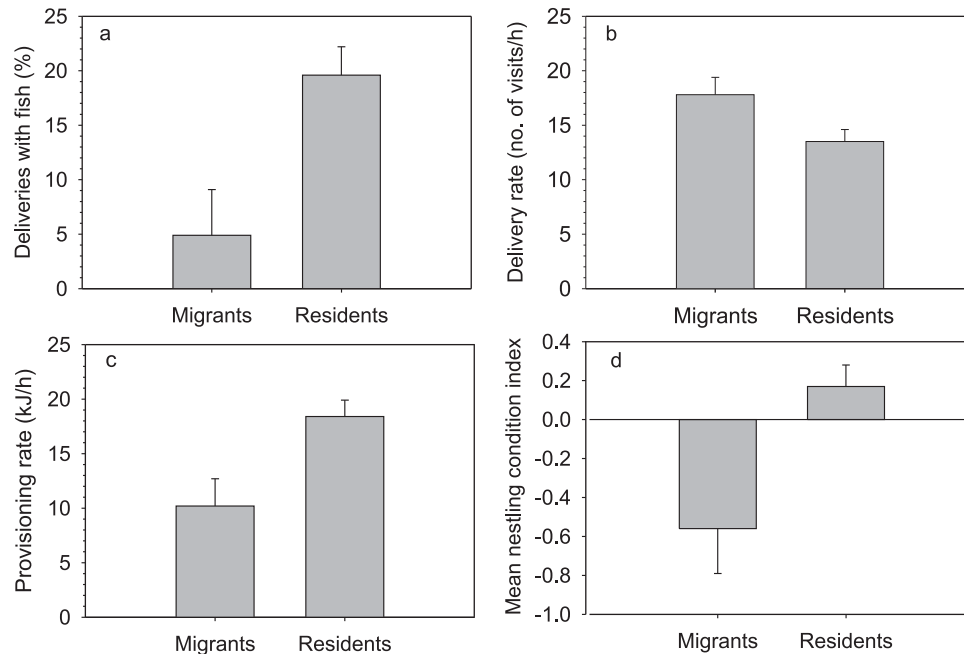
Table 2. Summary of isotopic values (mean ± SD) from prey and American Dipper (*Cinclus mexicanus*) feather samples.

|	$\delta^{15}N$ (‰) (*n*)		Statistics			
	River	Tributary	*t*	χ^2	df	*p*
Aquatic invertebrates	3.66±2.43 (6)	0.39±0.79 (5)	2.85	—	9	0.02
Salmon fry	11.53±1.58 (6)	9.89±0.88 (6)	2.2	—	10	0.05
Feather	9.04±1.78 (40)	4.39±0.73 (23)	—	139	1	<0.001

Note: Prey samples were collected from six sites on the main stem of the Chilliwack River and six sites on higher elevation creeks. Feather samples were obtained from nestlings provisioned by 12 sedentary pairs on the Chilliwack River and 8 migratory pairs on the tributaries.

Dippers; individuals that migrate to higher elevations to breed are less likely to initiate a second clutch following the success of their first breeding attempt and produce less offspring than sedentary individuals that breed at lower elevations (Gillis et al. 2008; Morrissey 2004). However, we found no evidence migratory individuals trade off the number of offspring produced over the course of a season with offspring quality. Migrants fed their offspring less fish and, although they compensated by feeding at a higher rate, had lower energetic provisioning rates. Nestlings in broods raised by migrants also had a lower mean nestling condition index than nestlings in broods raised by residents and, as a consequence, fledglings produced by migrants were less likely to survive their first winter.

Comparative studies have documented shifts in the life histories of species and populations breeding at higher elevations that result in a trade-off between the number and the quality of young produced. For example, Badyaev and Ghalambor (2001) found a strong negative relationship between the number of offspring and the level of parental care in phylogenetically paired taxa breeding at high and low el-

evations. Species breeding at higher elevations did not provision at a higher rate but provided fledged young with food for considerably longer than species breeding at low elevations. Extended postfledging care has been linked to higher juvenile survival and recruitment in several species (e.g., Green and Cockburn 2001; Middleton and Green 2008), suggesting reduced fecundity could be compensated for by higher juvenile survival. Similarly, Bears et al. (2009) found that while Dark-eyed Juncos breeding at high elevations produced fewer offspring their offspring were in better condition and more likely to survive until 25–30 days of age. In contrast, we found little evidence that breeding at higher elevations is associated with greater parental care and (or) the production of offspring with higher juvenile survival in American Dippers. Dippers breeding at higher elevations had lower energetic provisioning rates than sedentary conspecifics at lower elevations and produced offspring that were in worse condition that were less likely to survive until the following year. This differs slightly from previous work, which included a considerable amount of data from 2000 when reproductive success was at a 10 year high, that

Fig. 2. Relation between American Dipper (*Cinclus mexicanus*) nestling condition, estimated as the residual of a mass–tarsus regression, and the probability of being resighted after the end of January of the following year. The line shows the model predictions, the circles show the data binned into 2 g categories commencing at –12 g, and the numbers next to the circles show the sample size within each category.
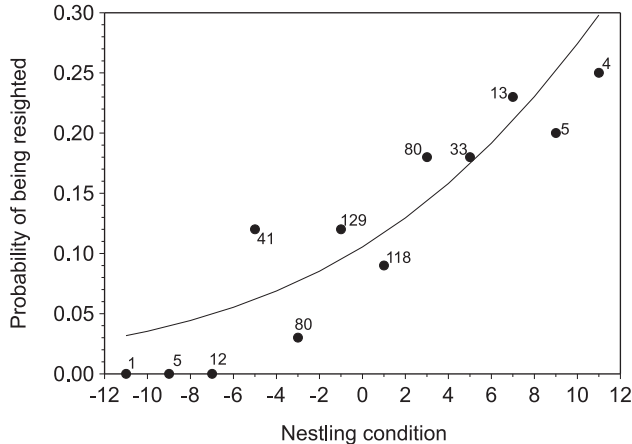
reported no difference in the mean nestling mass of broods raised by migratory and sedentary dippers (Morrissey 2004). Importantly, however, neither study provides any evidence to suggest dippers produce better quality offspring if they migrate to higher elevations to breed.

Breeding at higher elevations may not have been associated with increased parental care in this study because parental care was only examined during the nestling period. This is unlikely to be the case because parental provisioning rates decline considerably 1 week after fledging in American Dippers, and the offspring of migrants and residents are equally likely to have left their natal territory within 2 weeks (Middleton et al. 2007; Middleton and Green 2008). Furthermore, the positive correlation between our index of nestling condition and postfledging survival in this population suggests that postfledging parental care does not compensate for differences in the level of care provided during the nestling period. The absence of a trade-off between fecundity and parental care or juvenile survival suggests that life-history variation in this species is driven more by ecological factors, such as intraspecific competition, than selection pressures exerted by the different conditions at different elevations.

Our work has demonstrated that ecological conditions at high and low elevation influence both the number and the quality of offspring produced by migratory and sedentary American Dippers (Gillis et al. 2008; Morrissey 2004; this study). Seasonal variation in ecological conditions might also be expected to lead to seasonal variation in delivery rates, nestling diet, nestling condition, and postfledging survival. In this study we observed seasonal declines in the proportion of deliveries that included fish and showed that this led to seasonal declines in energetic provisioning rates of both residents and migrants. This may reflect differences in parental age and foraging ability, as young birds often initiate breeding later than old birds (Martin 1995) and may be less proficient foragers than older birds (Wunderle 1991).

Reduction in the amount of fish fed to nestling dippers could also be due to seasonal changes in the abundance and distribution of young salmonids, increased flow rates and turbidity owing to the spring snowmelt that makes foraging for fish more difficult, or seasonal increases in the abundance and (or) availability of aquatic invertebrates (Bramblett et al. 2002; Crisp 2000). Seasonal variation in provisioning behavior did not, however, lead to a corresponding seasonal decline in the mean nestling condition index of a brood. This result was not due to seasonal declines in brood size. The mean nestling condition index may have remained constant because the rising temperature (mean minimum and maximum daily temperatures for the Chilliwack River hatchery: 1 April = 2.8 and 10.7 °C; 30 June = 10.7 and 21.3 °C; National Climate Data and Information Archive, Environment Canada, Fredericton, New Brunswick, Canada) reduced thermoregulatory costs and nestling energetic demands (see Dawson et al. 2005). We also found no evidence for a negative relationship between hatch date and postfledging survival in American Dippers, in contrast to several other studies on passerines (reviewed in Daan et al. 1989). The higher survival of offspring raised by residents therefore appears to be due more to differences in nestling condition resulting from being fed a higher quality diet than differences in hatch date that allow their offspring more time to develop foraging skills prior to winter.

Altitudinal migration may allow individuals to track spatial and temporal variation in food availability (Loiselle and Blake 1991; Solórzano et al. 2000), or allow individuals to reduce the risk of nest predation (Boyle 2008; Fretwell 1980). Neither hypothesis appears to be a plausible explanation for altitudinal migration in American Dippers. Feeding observations and stable isotope analysis of feather samples, which reflect nestling diet over a longer period, show that offspring of migrants have a diet containing more invertebrates and less fish than the offspring of residents. This result is counter to what would be expected if altitudinal migration gave migratory dippers access to a higher quality diet or allowed higher energetic provisioning rates because fish have a higher energetic content and nutritional value (percent protein, phosphorus, and calcium) than aquatic invertebrates (Obermeyer et al. 2006), and nestlings fed a diet that contains more fish are in better condition (Obermeyer et al. 2006; this study). Previous work suggests it is also unlikely that altitudinal migration allows dippers to reduce the level of nest predation. Morrissey (2004) found that nests of migratory dippers are as likely to fail owing to predation as nests of residents.

Altitudinal migration in species with alternative migratory strategies may be an outcome of intraspecific competition. For example, in Carolina Juncos (*Junco hyemalis carolinensis* Brewster, 1886) competition for food at high elevations during the winter has been argued to force subordinate individuals to migrate to lower elevations (Rabenold and Rabenold 1985). In contrast, altitudinal migration in American Dippers has been argued to be an outcome of intraspecific competition for limited nesting sites at low elevations that forces the majority of individuals to either move to higher elevations to breed or forgo reproduction (Gillis et al. 2008). This hypothesis is supported by work showing that distributions of dippers are limited by suitable nest sites

(Loegering and Anthony 2006), residents have consistently higher annual productivity than migrants, and are predicted to have higher lifetime reproductive success (Gillis et al. 2008). This study demonstrates migrants do not compensate for their lower productivity by producing higher quality young. In fact, differences in the lifetime reproductive success of migrants and residents will have been underestimated because migrants produce lower quality offspring that are less likely to survive their first winter. This study therefore provides additional support for the hypothesis that altitudinal migration is a conditional strategy and that migrants are subordinate birds that are simply making the "best of a bad job" (Adriaensen and Dhondt 1990) by moving to higher elevations to breed.

Acknowledgements

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