Effect of altitudinal migration within a watershed on the reproductive success of American dippers

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Abstract: Distinct changes occur in the distribution of American dipper (*Cinclus mexicanus* Swainson, 1827) populations during the breeding season. Small numbers of American dippers remain resident on the wintering site, while the majority of birds make short altitudinal movements upstream. Therefore, American dippers breed over large elevation gradients within a watershed, using both the main river and its associated tributaries. I hypothesized that altitudinal migration of American dippers would affect their timing of breeding and ultimately their productivity. Additionally, since the main river and its tributaries differ in habitat, elevation, and nesting substrates, I hypothesized that these variables would also influence American dipper breeding performance. In the Chilliwack watershed of British Columbia, Canada, I followed 99 pairs of American dippers: 23 in 1999, 40 in 2000, and 36 in 2001, of which approximately 65% were residents and 35% were migrants. Resident pairs on the lower elevation river initiated nests earlier and a greater proportion had second broods, contributing to slightly higher nest success and annual productivity compared with migrants on tributaries. Reduced productivity was primarily associated with later onset of breeding, which increased the likelihood that nests were lost to predation or flooding and reduced the probability of initiating a second clutch. Timing of breeding was affected by migratory status and year, but elevation and habitat did not directly influence breeding performance.

Résumé : Il se produit des modifications caractéristiques de la répartition des populations de cincles d'Amérique (*Cinclus mexicanus* Swainson, 1827) durant la saison de reproduction. Un petit nombre de cincles d'Amérique demeurent sur les sites d'hiver, alors que la majorité des oiseaux font de courts déplacements en altitude vers l'amont. Les cincles d'Amérique se reproduisent sur un important gradient d'altitudes dans un bassin versant et ils utilisent à la fois le cours principal et ses tributaires associés. Mon hypothèse veut que la migration en altitude des cincles d'Amérique affecte le moment de leur reproduction et, par conséquent, leur productivité. De plus, puisqu'il y a des différences d'habitat, d'altitude et de substrats de nidification entre le cours principal et les tributaires, une seconde hypothèse veut que ces variables affectent aussi la performance reproductive des cincles d'Amérique. Dans le bassin versant de la Chilliwack, Colombie-Britannique, Canada, 99 couples de cincles d'Amérique ont été suivis, 23 en 1999, 40 en 2000 et 36 en 2001, dont environ 65 % étaient résidants et 35 % migrateurs. Les couples résidants dans la portion aval de la rivière commencent la nidification plus tôt et produisent une plus grande proportion de secondes portées, ce qui leur donne un succès au nid et une productivité annuelle légèrement supérieurs à ceux des couples migrateurs dans les tributaires. La réduction de la productivité est surtout reliée au début tardif de la reproduction qui augmente la probabilité de perdre des nids à cause de la prédation ou de l'inondation et diminue celle produire une seconde portée. Le moment de la reproduction est affecté par le statut migratoire et l'année; l'altitude et l'habitat n'affectent, cependant, pas directement la performance reproductive.

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Introduction

Population declines in many migratory bird species have led to considerable interest in the energetic and survival costs associated with long-distance migration (Klassen 1996; Sillett and Holmes 2002). Relatively few studies have examined the implications of short-distance altitudinal migration of birds. This strategy may be common for many resident birds across North America, particularly alpine-tolerant species (e.g., juncos, spotted owls, bluebirds, and ptarmigan) (Rabenold and Rabenold 1985; Laymon 1989; Martin 2001). Although migration is time consuming and energetically costly, this strategy may be advantageous if it allows birds to exploit areas with greater food abundance or superior nest sites in each season.

Timing of breeding can positively influence reproductive success of birds (Best and Stauffer 1980; Hartley and Shepard 1994; Kokko 1999). For some species, starting earlier increases individual productivity and offspring survival (Perrins 1965; Hochachka 1990; Verhulst and Tinbergen 1991). For birds that have multiple broods, earlier start dates may also provide an opportunity for renesting after a failed attempt or initiating a second clutch within the same season

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(Verboven and Verhulst 1996). Several studies of passerines demonstrate that nest location within different habitats can also affect variation in breeding parameters (Klomp 1970; Krebs 1971; van Balen 1973; Martin 1988; Sanz 1998). In addition, habitat features including nest site selection are known to strongly affect breeding performance (Martin and Roper 1988; Hoover and Brittingham 1998; Regehr et al. 1998). Individuals that occupy different habitats during the breeding season are likely to have access to different resources, including food and nest sites, that can potentially influence their reproductive success. Therefore, the requirement of good nesting sites and sufficient food abundance may conceivably drive some populations to migrate to higher elevations to gain access to additional breeding habitat. However, migration to those breeding sites could ultimately affect timing of breeding and overall reproductive success.

In early spring, large numbers of American dippers (*Cinclus mexicanus* Swainson, 1827) are observed migrating upstream from low-elevation wintering areas on rivers to higher elevation creeks (Price and Bock 1983; Campbell et al. 1997). This seasonal altitudinal migration is marked by a distinct change in the distribution of the population within a watershed during the breeding season, where small numbers of American dippers remain resident on the main river while the majority of birds make short altitudinal movements upstream (Morrissey et al. 2004). The effect of this migration is a dispersal of American dippers to different elevations on both the main stem of the river and the associated creeks, producing segregation between habitats.

Differences in breeding performance between resident and migrant American dippers may reflect delays in breeding that are associated with the migration period or changes in habitat associated with altitude. Reproductive success is also potentially influenced by the location of nest sites within a watershed because habitat and nesting substrates differ between the river and its tributaries. Rivers are typically wider, have a lower gradient, and have fewer cliffs and boulders than the associated creeks. In addition, the river, because of its lower elevation and higher flow, contains habitat that is without ice year-round. I hypothesized that the breeding performance of residents on the main river and that of migrants on higher elevation creeks would differ as a result of (*i*) migratory strategy, (*ii*) elevation, and (*iii*) habitat and nesting substrates. Therefore, the specific objective of this study was to determine the influence of altitudinal migration on reproductive success of American dippers within a watershed. In this study, I used timing of breeding, clutch size, brood size, number of broods, and annual female productivity as measures of breeding performance to evaluate differential reproductive success for river residents and creek migrants.

Materials and methods

Study area

The study was conducted in the Chilliwack River watershed (49°0′N, 121°4′W), located approximately 100 km east of Vancouver in the Cascade Mountain Range of southwestern British Columbia, Canada. The watershed contains first- through fourth-order streams and drains an area of approximately 1200 km^2. The river is fed by a lake at its upper end and is 43.5 km in length to the Vedder Crossing, where it becomes the Vedder River. The watershed has an elevation range of 20–2500 m, with American dipper nests located at 28–800 m. Other nests likely occurred at higher elevations but were not monitored for logistical reasons.

Data collection

I monitored the breeding biology of American dippers from early March through July 1999 to 2001, including all first, second, and replacement clutches. Over the 3-year period, 99 breeding pairs, comprising 64 resident and 35 migrant pairs, were monitored at least once per week throughout the breeding season. I attempted to capture and individually color-band the breeding adults to aid in future identification. Therefore, all pairs used in the analysis had at least one banded individual. Nests were located throughout the watershed by searching for pairs along continuous sections of river or creeks on foot or by following birds with nest material. All American dipper nests from both the river and the creeks had an equal chance of being detected using this method, since these areas were searched regularly throughout the season. Some nests were directly accessible for only part of the breeding season because of high water levels. These were subsequently removed from analysis of clutch or brood size but were monitored for timing of initiation, overall success in fledging young, and number of breeding attempts in the season.

Residents and migrants were classified based on their migratory behavior and breeding location within the watershed. Migrants were generally found nesting on tributaries but wintered elsewhere either on the main river or outside the watershed, whereas residents typically nested along the main river in the same location as they had wintered (Morrissey et al. 2004[2]). Migrant nests were monitored on seven different tributaries that were second- or third-order streams characterized by higher elevations, steeper gradients, fast water, a narrow path (3–20 m wide), coarse substrate, and an abundance of cliffs, boulders, and debris. Resident nests were generally on a single fourth-order river characterized by lower elevations, shallow gradients, slow-moving reaches, a wide and channelized path (26–62 m wide), and fewer areas with cliffs or boulders. Nest sites were categorized as one of six types: cliff ledges, rock boulders, undercut stream banks with exposed tree roots, bridges or other artificial structures, fallen logs or other woody debris, and other sites (on ground under rock and (or) concrete, and one nest on a tree limb).

Dates of clutch initiation, incubation, and hatching were typically known to within 1 day or were back-calculated assuming one egg was laid per day and the incubation period was 16 days (Price and Bock 1983; Kingery 1996). Clutch size was determined after laying was complete, i.e., when no new eggs had been added for 2 days. Brood size was recorded during routine banding when the nestlings were 12–14 days old (halfway through the nestling stage). Nest fate was considered successful if at least one chick fledged. If no fledglings were sighted and no evidence of nest failure was apparent, the fate of the nest was recorded as unknown. Since newly fledged American dippers are difficult to locate and often leave the nest asynchronously, I assumed that the total number of fledglings from successful nests was equal to the brood size at banding. This assumption is supported

Table 1. Summary of American dipper (*Cinclus mexicanus*) reproductive performance (clutch and brood sizes, overall nest success for all nest attempts, and annual productivity of pairs (number of young per season)) in the Chilliwack watershed of British Columbia, Canada, 1999–2001.

Year	Clutch size	Brood size	% successful	% failed	% unknown	Annual productivity
1999	4.11±0.15 (28)	2.42±0.34 (31)	64.9 (24)	35.1 (13)	0.0 (0)	3.39±0.57 (23)
2000	4.26±0.11 (50)	2.53±0.24 (58)	58.5 (38)	36.9 (24)	4.6 (3)	4.00±0.45 (40)
2001	4.47±0.13 (36)	1.79±0.30 (39)	55.4 (31)	39.3 (22)	5.4 (3)	2.67±0.46 (36)
All years	4.30±0.08 (114)	2.28±1.9 (128)	58.9 (93)	37.3 (59)	3.8 (6)	3.36±0.28 (99)

Note: All values are means ± SE or percentages. Sample size (*n*) is shown in parentheses.

by detailed observations of a subset of nests at the time of fledging, which showed that brood size at 12–14 days typically represented the number of fledged young.

Nest failure resulted from predation, flooding, nest collapse, egg failure, or nest abandonment and from unknown causes. Starvation of nestlings was never observed in this study as a cause of nest failure. I identified failure as a result of predation when eggs or young were broken, missing, or partially eaten and the nest was damaged. Flooded nests were identified as such when water levels rose above the level of the nest. Nest collapse was recorded when the domed nest structure caved in but eggs were still present. Nests were generally classified under the egg failure or nest abandonment categories if the eggs did not hatch because of infertility or insufficient incubation or if the nest was abandoned for any reason including death of an adult. If the nest was empty prior to fledging date and there was no evidence of what caused the failure, the fate of the nest was recorded as unknown.

Statistical analyses

Data on clutch size, brood size, elevation, and start date of incubation were continuous scale data and normally distributed, so either an independent two-sample *t* test or a one-way analysis of variance (ANOVA) with a Tukey multiple comparison test was used for comparison of means between migratory groups (river residents or creek migrants) and among years. To correct for year effects in comparisons of breeding start date and annual productivity of residents and migrants, I used a two-way ANOVA to include migratory status and year and report least square (LS) means to control for the other parameters. Data on nest success, multiple clutches (second and replacement), and nest site types were nominal scale data and were subsequently analyzed using χ^2 contingency tables with results reported as percentages.

A stepwise regression model was used to determine which variables (year, migratory status, elevation, start date of incubation of first clutches, and interaction terms) were important in explaining annual productivity (number of young/female per season). A multiple linear regression model was then used to determine which factors affected timing of breeding. The variables that influenced predation and flooding failures were analyzed using a logistic regression model with sequential elimination of nonsignificant terms. The initial predation and flooding models included start date of breeding, migratory status, elevation, year, and type of nest site but were reduced using stepwise procedures. Whole model results are presented where applicable in addition to the effect tests. Where comparisons were being made between migratory groups or for predictors in the regression models, data on a single pair were used only once each year by focusing on the female's first nest attempt. Data from each year were treated as independent, as the majority of pairs were sampled in only one year. Measures are presented as means ± SE unless otherwise stated. The significance level was set at 0.05 for all analyses. Statistical analyses were performed using the software JMP IN® version 4.0 (SAS Institute Inc.).

Results

General breeding biology

The mean Julian date (1 January = day 1) for starting incubation of first clutches was 95.6 ± 1.5 days (5 April) but was significantly different among study years ($F_{[2,93]} = 7.52$, $P < 0.001$). The winter of 1999 had a record snowfall that lasted well into March, resulting in a later start date of incubation in 1999 (104.0 ± 2.7 days = 14 April) compared with the winters of 2000 and 2001 (2000, 90.1 ± 2.3 days = 31 March; 2001, 94.6 ± 2.3 days = 5 April).

There was no effect of year on mean clutch size ($F_{[2,111]} = 1.99$, $P = 0.14$) and mean brood size ($F_{[2,125]} = 1.89$, $P = 0.16$) (Table 1). The proportion of breeding pairs with second and replacement clutches was also not different among years ($\chi^2_4 = 1.9$, $P = 0.8$). Repeat clutches tended to be smaller, but clutch and brood sizes of second and replacement clutches were not significantly different from those of first clutches (clutch size, $F_{[2,111]} = 1.12$, $P = 0.3$; brood size, $F_{[2,125]} = 1.55$, $P = 0.2$).

In total, 158 nest attempts, including first, second, and replacement clutches, were followed over the 3-year period. For all years combined, 99 nests (63%) were first clutches, 38 (24%) were second clutches, and 21 (13%) were replacements of failed clutches. Overall, 59% of the nesting attempts resulted in successfully fledged young, with no differences in overall nest success among years ($\chi^2_4 = 3.7$, $P = 0.5$) (Table 1). Over the course of the entire breeding season, 73.2% of pairs successfully fledged at least one young. All pairs combined produced an average of 3.4 ± 0.3 young per season (range 0–10), and the number of young per season did not differ significantly among study years ($F_{[2,94]} = 2.18$, $P = 0.12$) (Table 1).

Effect of migratory behavior

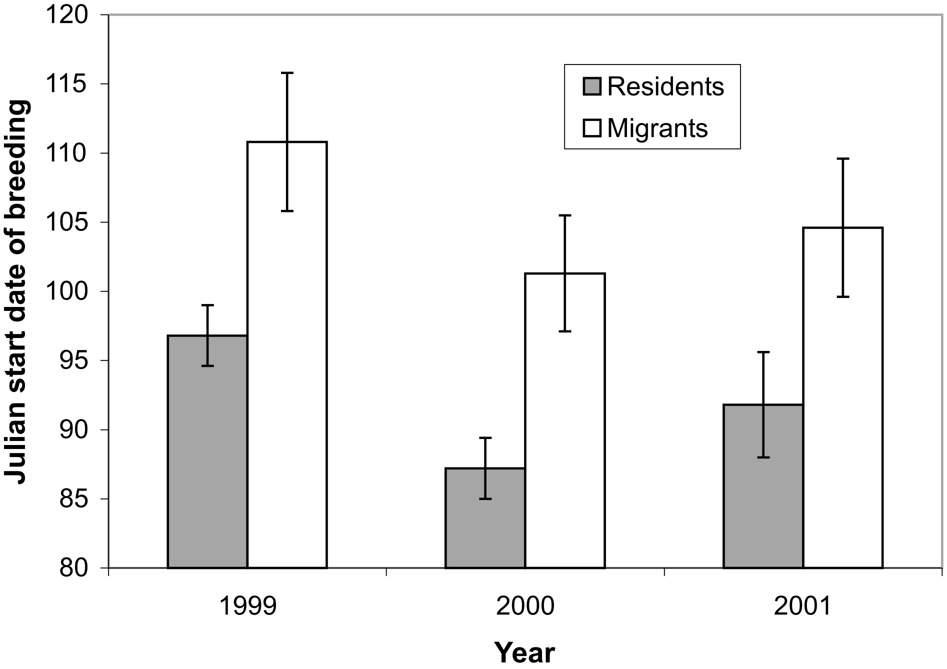
Data comparing the breeding performance of resident and migrant pairs are summarized in Table 2. Creek migrants initiated breeding significantly later than river residents in every year of the study ($F_{[3,88]} = 8.76$, $P < 0.0001$) (Fig. 1). However, clutch size ($t_{[74]} = -0.93$, $P = 0.4$) and brood size ($t_{[83]} = -1.6$, $P = 0.1$) of creek migrants were not signifi-

Table 2. Summary of reproductive parameters measured in comparing success of resident and migrant American dipper pairs on the Chilliwack River and its tributaries in British Columbia, Canada, 1999–2001.

Parameter	Residents	Migrants	Significance (*p*)
Number of pairs (*N*)	64	35	
Mean elevation (m)	179±13	285±18	<0.0001
Clutch size	4.4±0.1	4.2±0.1	ns
Brood size	2.7±0.3	2.0±0.4	ns
Nestling mass (g; LS mean)	46.3±0.7	46.1±0.9	ns
Annual productivity (no. young/female; LS mean)	3.7±0.4	2.8±0.5	ns
Start date of incubation (Julian date; LS mean)	92±2 (2 April)	106±3 (16 April)	<0.0001
% successful	67.2	53.1	ns
% pairs with second clutches	49.2	17.6	<0.0002
% pairs with replacement clutches	10.8	41.2	<0.0002

Note: Least square (LS) means are reported to correct for year effects on productivity and start date of incubation and for brood size and age effects on nestling mass.

Fig. 1. Comparison of mean (±SE) Julian start date (1 January = day 1) of incubation for first clutches of resident and migrant American dippers (*Cinclus mexicanus*) in the Chilliwack watershed in 1999, 2000, and 2001. Residents had significantly earlier breeding start dates than migrants in every year of the study ($P < 0.001$).



cantly different from those of river residents (Table 2). In addition, nestling mass did not differ by location when corrected for age at weighing and size of the brood (LS mean; residents, 46.3 ± 0.7 g; migrants, 46.1 ± 0.9 g) ($F_{[1,228]} = 0.19$, $P = 0.7$) (Table 2).

The individual nest success of migrant first clutches (53.1%) appeared lower than that of resident first clutches (67.2%), although the difference was not statistically significant ($\chi^2_1 = 1.8$, $P = 0.18$) (Table 2). The percentage of resident pairs that had second broods was higher than the proportion of migrants with second broods ($\chi^2_2 = 17.56$, $P < 0.0002$). In addition, residents had fewer replacement clutches following failed nesting attempts compared with migrants (Table 2). On average, resident pairs produced 3.7 ± 0.4 young per season, whereas migrants produced 2.8 ± 0.5 young per season. After correcting for any year effects, this difference was nonsignificant ($F_{[3,93]} = 2.25$, $P = 0.09$) (Table 2).

A stepwise regression was used to determine which variables were important in explaining the annual productivity or number of young produced per female during the breeding season. Breeding start date had a strong negative effect on annual productivity ($F_{[3,87]} = 19.5$, $P < 0.0001$) (Fig. 2). Annual productivity also varied with the year of the study ($F_{[3,87]} = 4.3$, $P = 0.04$). Migratory status, elevation, and other interaction terms had no effect. Further regression analysis of the factors that affected the start date of breeding demonstrated that both migratory status ($F_{[1,92]} = 36.2$, $P < 0.0001$) and year ($F_{[2,92]} = 6.6$, $P = 0.002$) were significant predictors of when American dippers started breeding. Migrants initiated breeding later than residents (migrants, LS mean = 106 ± 3 days; residents, LS mean = 92 ± 2 days) and

Fig. 2. Annual productivity of American dippers in the Chilliwack watershed in 1999–2001, measured as the number of young produced per female during a breeding season in relation to the Julian start date of incubation for first clutches.

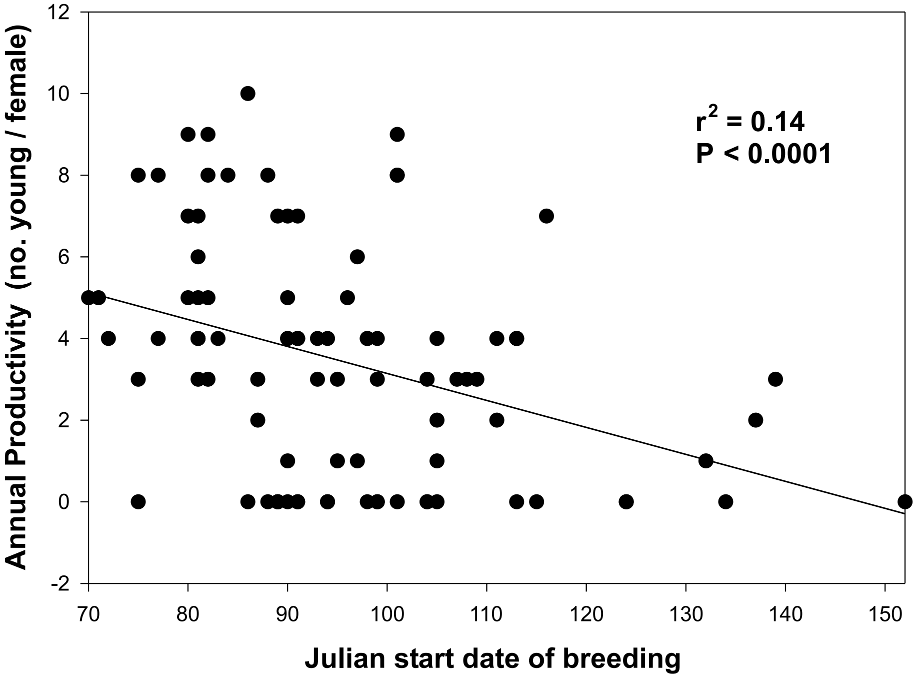


Table 3. Comparison of nest site success, relative frequency of nest site use by residents and migrant American dippers, and proportion of nest failures attributable to predation or flooding for each nest site type in the Chilliwack watershed, British Columbia, Canada, 1999–2001 (see Materials and methods for explanation of nest site classification).

		Frequency of use (%)		Cause of nest failure (%)	
Nest site type	Nest success (%)	Residents	Migrants	Predation	Flooding
Cliffs	63.6	26	52	38	43
Stream banks, roots	67.9	24	6	25	0
Boulders	39.1	13	19	4	43
Artificial	56.3	30	2	21	0
Logs, wood debris	56.3	4	22	8	14
Other	75.0	4	0	4	0
Total (all nest sites)	58.9			40.7	23.7

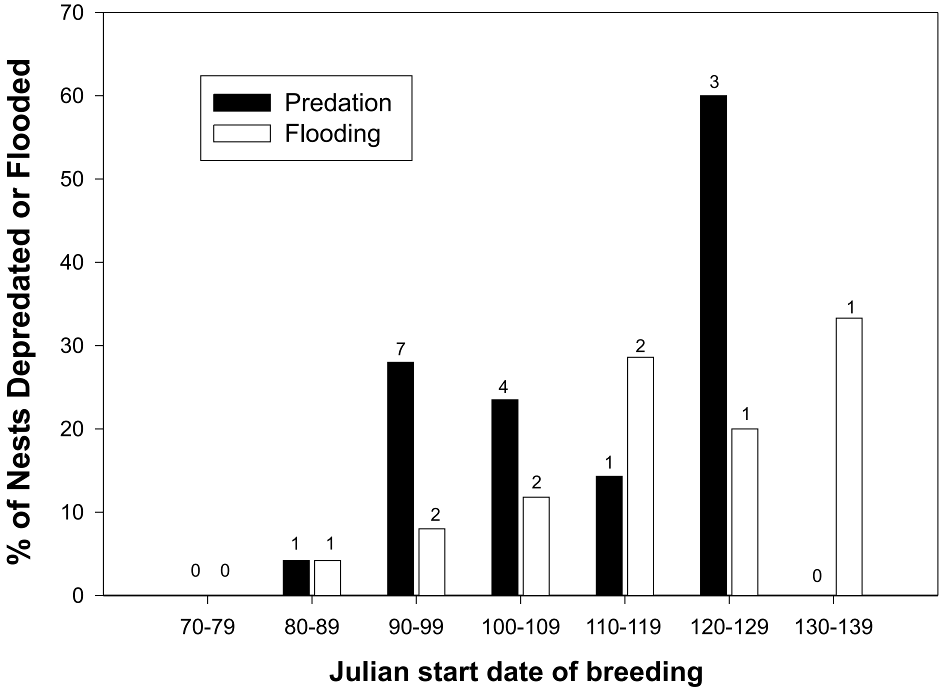
in 1999 breeding was initiated later than in 2000 or 2001. Therefore, American dippers that started incubating first clutches later, either because of migration or because of year effects, had lower annual productivity. Breeding location (river or creek) and elevation had no additional effect on annual productivity.

Nest site characteristics and causes of failure

The relative use of nest site types differed significantly between migrants and residents ($\chi^2_5 = 49.3$, $P < 0.0001$) (Table 3). Specifically, migrant American dippers on creeks used predominantly cliff sites, logs and (or) woody debris, and boulders. Resident American dippers on the main river used a wider variety of nest sites including artificial structures, cliffs, stream banks, and boulders, but there was no clear prevalence of use at any particular site.

The most common causes of nest failure were predation and flooding (Table 3). The cause of failure for all nest sites was not significantly different between residents and migrants ($\chi^2_4 = 6.5$, $P = 0.17$). However, the incidence of flooding was notably higher for creek migrants (33%) than for river residents (17%). There was a general trend towards increasing risk of both predation and flooding for first breeding attempts with later breeding start dates. Birds that nested early (prior to day 88–89) avoided both predation and flooding. After that date, proportions of failures attributable to these two sources increased (Fig. 3). A logistic regression model was used to determine the variables that predicted predation and flooding of first clutches. Both whole models were significant (predation model, $\chi^2_8 = 14.7$, $P = 0.04$; flooding model, $\chi^2_8 = 17.6$, $P = 0.02$). For the predation model, only start date of breeding had a significant effect ($P = 0.01$), whereas nest site type and year also contributed to the overall model. Flooding was best predicted by start date of breeding, year, elevation, and nest site type; however, as in the predation model, only the start date of breed-

Fig. 3. Percentage of American dipper nests that failed because of predation (n = 16) or flooding (n = 9) for each of seven 10-day intervals during the breeding season. Dates shown are Julian dates (1 January = day 1) and range from day 70, the earliest date that initiation of incubation of first clutches was recorded, to day 137, the latest date that initiation of incubation was recorded. Numbers above bars indicate the number of nests in each time interval that failed because of predation or flooding.



ing was a significant individual effect (P = 0.05). Nest site type greatly contributed to the overall strength of the flooding model. In fact, the sites that most commonly flooded were boulders (43%), cliffs (43%), and logs and (or) woody debris (14%), which correspond to the sites primarily occupied by the later breeding creek migrants (Table 3).

Discussion

American dippers generally have two migratory strategies: altitudinal migration to higher elevation tributaries or year-round residency on the lower elevation rivers. No previous studies of American dippers have identified differential reproductive success at different locations within a watershed. In this study, I demonstrate that altitudinal migrants breeding on tributaries initiated breeding later, had a higher frequency of replacement clutches, and had fewer second broods than resident pairs on the main river. Timing of initiation of breeding was the most significant effect on annual productivity. However, I found no additional effect of being a resident or a migrant over the timing of breeding in predicting productivity. Instead, migratory status was an important predictor of when birds initiated breeding. Since nests of migrants had the same numbers of eggs and nestlings as those of residents, and nestling mass was identical at the two locations, observed differences in productivity were likely not caused by variation in food supply. Instead, the differences were more likely caused by extrinsic factors such as flooding and predation, which resulted in a larger total number of nest failures.

Nest success of first clutches did not differ significantly between residents and migrants, but more nest failures were observed for the creek migrants given the larger proportion of replacement broods initiated by migrants. Resident American dippers that start breeding earlier may be able to produce more young per season by initiating more second broods and having fewer replacement broods. Limitations of sample size in the migrant group (n = 35 pairs) may have decreased statistical power of the comparisons of brood size, annual productivity, and success of nest attempts between residents and migrants. However, average annual productivity was 1.3 times higher for residents. This difference is likely biologically relevant but was not detected using the present sample. Timing of breeding was clearly different between the migratory groups and had a strong influence on productivity. In fact, American dippers that bred even slightly later in the season were at greater risk for nest failures attibutable to flooding or predation. Flooding was the second most common cause of nest failure and was found to be almost two times higher for the later breeding migrants. Furthermore, it is now widely recognized that in many breeding passerines the earliest broods generally have higher survival and higher recruitment rates (Perrins 1965; Hochachka 1990). Ormerod and Tyler (1993) determined that postfledging survival of European dippers varied significantly during the breeding season, with most survivors coming from nesting attempts during the peak period of hatching and fewer coming from attempts later in the season. Therefore, American dippers that can begin nesting early will have the opportunity to avoid predation and flooding, produce more double broods, and perhaps increase their brood's chance for survival.

Other dipper researchers have found positive relationships between elevation and timing of breeding (Bakus 1959;

Goodge 1959; Sullivan 1973; Ealey 1977; Tyler and Ormerod 1994). Nesting in dippers likely begins soon after the females have sufficient food for egg production (Perrins 1970; Drent and Daan 1980). It is reasonable that dippers in high-elevation territories will have delayed access to food resources because of ice cover and colder temperatures. However, I found no direct effect of elevation on productivity or timing of breeding after controlling for migratory strategy. In fact, river residents occupied territories at a wide range of elevations, which overlapped those of altitudinal migrants. Therefore, delays in breeding were a result of the migration period, when birds moved from wintering sites on the river to higher elevation tributaries. Delays in breeding were not caused by elevation per se, but they are a consequence of altitudinal migration. Therefore, altitudinal migration can influence American dipper breeding performance, as territory and mate acquisition of migrating birds would occur later, relative to birds that breed and winter in the same location.

Resident and migrant American dippers that occupy river or creek habitats during the breeding season may have access to different resources, including food and nest sites, that can potentially influence their reproductive success (Svensson and Nilsson 1995). However, migratory behavior did not appear to be related to food supply or improved habitat quality. There was no difference in clutch or brood size between migrants and residents, and although food abundance was not measured directly, nestling mass was identical at the two breeding locations. It has been suggested that competition for limited nest sites may force the majority of the population to disperse over a wider area during the breeding season (Price and Bock 1983; Tyler and Ormerod 1994). Densities of breeding pairs along the main stem of the Chilliwack River were relatively high (approximately 2.41–2.98 birds km^{-1}) (C. Morrissey, unpublished data) compared with reports in the literature of <1.0 to 1.7 birds km^{-1} (Price and Bock 1983) and 1.16–1.22 birds km^{-1} (Ealey 1977). Given these relatively high densities, competition may force many American dippers to seasonally migrate onto tributaries where nest sites such as cliffs and boulders are more abundant. This ultimately results in a segregation of birds between river and creek habitats but without any significant gain in habitat quality. The presence of migrant birds suggests that these individuals may be subordinate to residents either because of age or lack of experience. However, after color-marking 272 hatch-year American dippers during the course of the study, we found that juveniles recruited equally as residents and migrants and were capable of breeding successfully in their first year regardless of migratory status (C. Morrissey, unpublished data; Morrissey et al. 2004). Experimental increases in the number of nest sites available along the main river through addition of nest boxes would reveal whether nest site limitation is a significant cause of spring altitudinal migration.

Migratory status influenced not only timing of breeding but also the distribution of nest sites used by residents and migrants. River and creek locations differ in the type of substrates available for nesting sites, probably because of the differences in habitat. The creeks had more natural cliffs and boulders and tended to be narrower with steeper gradients. Consistent with the habitat, migrant birds used cliffs, boulders, and fallen logs or woody debris with greater frequency than the resident birds. Those specific sites were also found to be more susceptible to flooding during high water events. In general, nest site type was an important variable in predicting flooding and predation events. Most other studies of American dippers report a similar distribution of nest sites and common causes of nest failure, mainly predation and flooding (Ealey 1977; Price and Bock 1983; Osborn 1999). For many species of passerines, nest predation remains the principal cause of nest losses across a broad diversity of habitats and locations, accounting for an average of 80% of nest losses (Ricklefs 1969; Martin 1993). But for birds nesting near water, flooding is also a significant cause of nest failure (Burger 1985). Therefore, quantifying nest site availability for resident and migrant American dippers occupying different habitats may be important for predicting nest losses due to flooding and predation events.

In conclusion, altitudinal migration had a negative effect on reproductive timing and overall productivity of American dippers. Resident birds were able to gain access to mates and breeding sites significantly earlier than birds that migrated onto the creeks. Thus, resident American dippers had greater opportunity to avoid predation and flood events and to initiate second clutches. Although reproductive success was not directly related to migratory strategy, residents may benefit from improved survival, higher lifetime reproductive output, or greater survival of their offspring. Future research on survival costs of being a permanent resident or altitudinal migrant and investigations into the factors that influence individual migration strategies may shed greater light on our current understanding of altitudinal migration.

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