

# 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 likeli-

(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 ulti-



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,  $46.3 \pm 0.7$  g; migrants,  $46.1 \pm 0.9$  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





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<sup>-1</sup>) (C. Morrissey, unpublished data) compared with reports in the literature of <1.0 to 1.7 birds km<sup>-1</sup> (Price and Bock 1983) and 1.16–1.22 birds km<sup>-1</sup> (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, boul-

ders, 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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