Correlates of postfledging survival, the timing of dispersal, and local recruitment in American Dippers

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siblings if the benefits of extended philopatry outweigh the

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also likely to influence the timing of dispersal. Studies have shown that the early acquisition of foraging skills can allow individuals to become independent sooner (Yoerg 1998) and disperse earlier (Alonso et al. 1998), while an increased reliance on being provisioned may delay independence (Heinsohn 1991). Environmental conditions that can influence the timing of dispersal include habitat quality, prey density, and the number of siblings within a territory (Newton and Marquiss 1983; Wiens et al. 2006). Dispersal may also be delayed by modifications to the landscape that restrict the movement of some species (e.g., Lens and Dhondt 1994, but see Currie and Matthysen 1998).

Studies showing that variation in the timing of dispersal has consequences for survival, recruitment, and subsequent reproductive success remain scarce, but they are gradually accumulating. For example, female Superb Fairywrens (*Malurus cyaneus* (Ellis, 1782)) either disperse 1–2 months after fledging or delay dispersal until the onset of the next breeding season (Mulder 1995). Cockburn et al. (2003) subsequently demonstrated that female Fairywrens that disperse early are far more likely to obtain a breeding vacancy than those that delay dispersal. Male Brown Thornbills (*Acanthiza pusilla* (White, 1790)) may also disperse soon after reaching independence or delay dispersal for several months. In this species, however, individuals that delay dispersal were more likely to obtain a breeding vacancy than individuals that dispersed early (Green and Cockburn 2001). Male Siberian Jays (*Perisoreus infaustus* (L., 1758)) also obtain fitness benefits from delaying dispersal because remaining in their natal territory allows them to queue for high-quality habitat. Acquiring a superior territory increases their lifetime reproductive success compared with males that disperse early but occupy breeding vacancies in low-quality habitat (Ekman et al. 1999, 2002).

In this paper, we investigate potential causes of variation in the timing of natal dispersal in American Dippers (*Cinclus mexicanus* Swainson, 1827) and evaluate how dispersal decisions affect local recruitment. Specifically, we (*i*) monitored marked fledglings to determine when they left their natal territory, (

(standing, preening). We also recorded the number of times a fledgling was fed during the focal observation. Foraging behaviour and parental provisioning did not vary over the 5 day period (Middleton 2006), so foraging scores (propor-

by day 14 (nestling size: $\chi^2_{[1]} = 0.0$, $P = 0.99$; nestling condition: $\chi^2_{[1]} = 0.12$, $P = 0.73$, age at fledging: $\chi^2_{[1]} = 0.17$, $P = 0.68$). The date of fledging or year did not influence the probability of dispersal (date: $\chi^2_{[1]} = 0.95$, $P = 0.33$, year: $\chi^2_{[2]} = 1.28$, $P = 0.28$). Neither the location of the territory, which reflects the migratory status of the parents, nor the social environment had any effect on whether fledglings had left their natal territory by day 14 (location, $\chi^2_{[1]} = 0.32$, $P = 0.57$, number of siblings $\chi^2_{[1]} = 0.04$, $P = 0.85$). For both sexes, individuals that spent more time foraging were more likely to have dispersed by day 14 ($\chi^2_{[1]} = 3.97$, $P = 0.05$; sex $\times$ foraging score interaction: $\chi^2_{[1]} = 0.52$, $P = 0.47$; Fig. 2). The provisioning rate of the parents, however, had no effect on whether a fledgling had left their natal territory by day 14 ($\chi^2_{[1]} = 0.71$, $P = 0.40$).

Individuals that dispersed by day 14 spent less time in their natal territory if they fledged early in the season ($\chi^2_{[1]} = 11.6$, $P = 0.001$) or fledged at an older age ($\chi^2_{[1]} = 4.38$, $P = 0.04$). Fledglings produced in 2005 also spent longer in their natal territory (predicted mean $\pm$ SE: 11.1 ± 0.6 days) than fledglings produced in 2003 or 2004 (2003: 8.6 ± 0.5 days; 2004: 9.6 ± 0.5 days; $\chi^2_{[2]} = 9.44$, $P = 0.01$). The sex of an individual ($\chi^2_{[1]} = 0.0$, $P = 0.99$) and their size or condition as a nestling had no effect on the timing of departure (nestling size: $\chi^2_{[1]} = 0.34$, $P = 0.56$; nestling condition: $\chi^2_{[1]} = 0.71$, $P = 0.40$). The location of the territory and the number of siblings also had no effect on when fledglings left their natal territory (location: $\chi^2_{[1]} = 0.0$, $P = 0.97$; number of siblings: $\chi^2_{[1]} = 0.02$, $P = 0.91$). Neither the amount of time an individual spent foraging ($\chi^2_{[1]} = 0.14$, $P = 0.70$) nor the parental provisioning rate ($\chi^2_{[1]} = 0.39$, $P = 0.54$) influenced how much time early-dispersing fledglings spent in their natal territory.

Local recruitment

Ten of the 82 fledglings that survived to day 5 were re-sighted at least 10 months after fledging, an age when they could recruit into the breeding population (males 7/51, females 3/31). All 10 were located in the year after fledging and no additional birds were resighted in subsequent years. Three males obtained permanent breeding territories on the main stem of the river and seven individuals overwintered on the main stem of the river but left in March presumably to seek breeding territories at higher elevations. Of the individuals that left the river in March, one female was known to breed on a creek territory, while two males and two females were resighted on the river in subsequent winters. Only one factor influenced local recruitment. Fledglings that delayed dispersal were more likely to recruit into the local population than those departing 6–13 days after nest departure ($\chi^2_{[1]} = 4.25$, $P = 0.04$; Fig. 3). Fledgling sex, their size, or condition as a nestling, as well as their age at fledging, all had no effect on local recruitment (sex: $\chi^2_{[1]} = 0.29$, $P = 0.59$; nestling size: $\chi^2_{[1]} = 0.05$, $P = 0.82$; nestling condition: $\chi^2_{[1]} = 0.04$, $P = 0.84$; fledging age: $\chi^2_{[1]} = 0.0$, $P = 0.95$). The probability of local recruitment did not vary between years ($\chi^2_{[2]} = 0.11$, $P = 0.90$), with fledging date ($\chi^2_{[1]} = 1.25$), or differ depending on the location of the territory ($\chi^2_{[1]} = 0.04$, $P = 0.85$) or the number of siblings alive on day 5 ($\chi^2_{[1]} = 0.0$, $P = 0.99$). After controlling for dispersal strategy, neither the amount of time spent foraging nor the parental provisioning rate in the first 5 days after fledging had a significant effect on local recruitment (time foraging: $\chi^2_{[1]} = 1.06$, $P = 0.30$; parental provisioning rate: $\chi^2_{[1]} = 2.22$, $P = 0.14$).

Discussion

less time foraging were less likely to have dispersed within 14 days of fledging than females and individuals that foraged more. For juvenile American Dippers that did disperse within 14 days, those that fledged early in the season and at an older age spent less time in their natal territory. In contrast, the habitat in which juveniles were raised and the date or year in which they fledged had little effect on the dispersal behaviour of juvenile American Dippers. We also found that the dispersal strategy of an individual had an effect on local recruitment, suggesting at least during the years of this

more likely to obtain a breeding territory than males that dispersed as soon as they reached independence (Green and Cockburn 2001). Similarly, male Siberian Jays that delayed dispersal for a year or more obtained higher quality territories and achieved higher lifetime reproductive success than males that dispersed in their first summer (Ekman et al. 1999). Our study showed that American Dippers that delayed departure were far more likely to be resighted in or after March of the year following hatch, at which point juveniles have either acquired a permanent territory in the main stem of the river or start to leave to seek breeding territories at higher elevations. This result suggests that an extended period of natal philopatry also enhances local recruitment in American Dippers.

Our study may have exaggerated the benefits of delayed dispersal because we assumed that all fledglings that were last seen in their natal territory between day 5 and day 13 dispersed when some of them may have died. However, 30 of the 38 fledglings that were assumed to have dispersed between days 6 and 13 would need to have died for the local recruitment of early dispersers to be equal to that of those who delayed dispersal. This appears extremely unlikely given that the mortality rate during this period would be more than three times the observed mortality during the first 5 days after nest departure.

The benefits of delayed dispersal would also be exaggerated if juvenile American Dippers that delay dispersal travel shorter distances and are simply more likely to be resighted. Although it is likely we did not resight all juveniles that survived to recruitment age, we do not believe that our estimates are likely to be biased because we resighted over 10% of dispersing individuals, females that typically disperse farther were as likely to be detected as males, and the distances juveniles travelled to winter or breeding locations were small (mean distance = 4.1 km; range = 0.4–18.3 km) relative to the distances that individuals could have moved and been detected (up to 40 km). Our study, and studies on other species (Strickland 1991; Alonso et al. 1998; Ekman et al. 1999; Green and Cockburn 2001), suggest that delayed departure may therefore have general benefits for the young of both cooperative and noncooperative bird species.

Although delayed dispersal can have fitness benefits in some species, several studies have shown that individuals can obtain fitness benefits from reducing the amount of time spent in their natal territory. Individuals that depart early sometimes disperse shorter distances (Nilsson 1989; Alonso et al. 1998) and can be more likely to recruit (Verboven and Visser 1998). Marsh Tits (*Poecile palustris* (L., 1758)) that dispersed shortly following fledging benefited by acquiring a dominant position in a winter flock (Nilsson and Smith 1988) and moving shorter distances to find a breeding vacancy (Nilsson 1989). In our study despite the apparent advantage of extended natal philopatry, nearly 50% of birds dispersed within 14 days. We found little evidence to suggest that these individuals were forced to disperse by their parents or siblings, and in fact individuals that fledged early in the year or at an older age, and are likely to be more competitive, dispersed sooner than those that fledged later or at a younger age. This suggests that there may be benefits to early dispersal at least in some years that we were unable to detect over the 3 years of this study. Over the course of this study, adult overwinter survival was below average and local population density was lower than that observed between 1999 and 2002 (Gillis et al. 2008; D.J. Green, unpublished data), providing conditions where competition for local vacancies is low and delayed dispersal might be expected to be advantageous. This raises the possibility that the fitness consequences of early and delayed dispersal in American Dippers may differ in years when adult survival and local population densities are high.

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