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

Holly A. Middleton and David J. Green

Abstract: Natal dispersal is a complex process that involves decisions about when to leave the natal territory, how to move through the landscape, and where to settle. We investigated what factors influence the timing of dispersal and local recruitment of American Dippers (*Cinclus mexicanus* Swainson, 1827) in Chilliwack, British Columbia. We monitored 102 fledglings from 30 broods between 2003 and 2005. Survival to 5 days after fledging was high (>80%), but individuals fledging early in the season and at an older age had higher survival than those fledging later and younger. Fifty-four percentage of surviving fledglings dispersed within 14 days of nest departure. Females and individuals that spent more time foraging were more likely to disperse within 14 days than males and individuals that foraged less. For those that dispersed, individuals that fledged early in the season and at older ages spent less time in their natal territory. Approximately 10% (10/82) of dispersing individuals were known to recruit locally. Local recruitment of individuals that delayed dispersal was higher than local recruitment of individuals dispersing early. Our study demonstrates that fitness benefits associated with extended natal philopatry are not restricted to cooperatively breeding birds.

Résumé : La dispersion après la naissance est un processus complexe qui implique des décisions sur quand quitter le territoire natal, comment se déplacer à travers le paysage et où s'établir. Nous avons étudié les facteurs qui déterminent le moment de la dispersion et le recrutement local chez des cincles d'Amérique (*Cinclus mexicanus* Swainson, 1827) à Chilliwack, Colombie-Britannique. Nous avons suivi 102 jeunes à l'envol provenant de 30 couvées entre 2003 et 2005. La survie jusqu'à 5 jours après l'envol est élevée (>80 %), mais les petits qui prennent leur envol tôt dans la saison ou à un âge plus avancé ont des taux de survie plus grands que ceux qui s'envolent plus tard ou à un âge moins avancé. Cinquante-quatre pourcentage des petits qui survivent à l'envol se dispersent en moins de 14 jours après le départ du nid. Les femelles et les individus qui passent plus de temps à s'alimenter sont plus susceptibles de se disperser en dedans de 14 jours que les mâles et les individus qui s'alimentent moins. Chez ceux qui se dispersent, les individus qui prennent leur envol tôt dans la saison ou à un âge plus avancé passent moins de temps dans leur territoire natal. Nous avons observé qu'environ 10% (10/82) des individus qui se dispersent s'intègrent à la population locale. Le recrutement local des individus qui retardent leur dispersion est plus élevé que le recrutement local des individus qui se dispersent tôt. Notre étude démontre que les bénéfices de fitness associés à une philopatrie natale prolongée ne sont pas restreints aux oiseaux qui se reproduisent de manière coopérative.

[Traduit par la Rédaction]

Introduction

Natal dispersal can be thought of as a three-step process that requires individuals to make a series of decisions as they leave their natal territory, move through the landscape, and finally settle in a new location. Numerous studies have explored why some individuals in cooperatively breeding species defer dispersal and forego independent reproduction (Koenig et al. 1992), described and evaluated explanations for sex differences in dispersal distances (Greenwood and Harvey 1982; Clarke et al. 1997), and examined potential cues that individuals use to select habitat (Cody 1985; Jones 2001; Doligez et al. 2002). Fewer studies have evaluated the causes and consequences of variation in the timing of dispersal in obligate dispersers, even though there is considerable variation in the timing of natal departure both among and within species.

In birds, the timing of dispersal can be influenced by both the phenotype of the individual and the environmental conditions. Studies have frequently shown sex differences in when individuals leave their natal territory (e.g., Alonso et al. 1998; Green and Cockburn 2001). Individuals of high competitive ability or social status may also disperse relatively early if this allows them greater access to high-quality territories or favourable habitat (Nilsson and Smith 1985, 1988). For example, dominant juvenile Western Screech Owls (*Megascops kennicottii* (Elliot, 1867)) disperse before their subordinate siblings (Ellsworth and Belthoff 1999). In contrast, dominant individuals may disperse later than their siblings if the benefits of extended philopatry outweigh the benefits of early dispersal (e.g., Strickland 1991; Ekman et al. 2002). The behaviour of juveniles and their parents is

H.A. Middleton[1,2] and D.J. Green. Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby BC V5A 1S6, Canada.

[1]Corresponding author (e-mail: Holly.Middleton@ec.gc.ca).
[2]Present address: Institute of Urban Ecology, Douglas College, P.O. Box 2503, New Westminster, BC V3L 5B2, Canada.

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, (*ii*) examined how characteristics of the individual and their environment influenced departure decisions, and (*iii*) determined the effects of departure decisions on local recruitment by juveniles.

Materials and methods

Study area and study species

We studied American Dippers within the Chilliwack River watershed (49°0′N, 121°4′W), which is located approximately 100 km east of Vancouver in the Coast Mountain Range of southwestern British Columbia, Canada. The Chilliwack River is approximately 43.5 km long, is fed from the east by Chilliwack Lake, and drains an area of approximately 1200 km². Breeding was monitored at eight locations on the main stem of the river and on five tributaries (monitored section ranged from 1 to 6.5 km long). This population of American Dippers consisted of both migratory and sedentary (resident) individuals. Migrants make seasonal movements between breeding areas on higher altitude tributaries and wintering areas on the main stem of the river. Resident individuals retain multipurpose territories on the

main stem of the river year-round (Morrissey 2004). In this population, breeding territories range in length from 0.2 to 0.8 km and natal dispersal distances range from 0.4 to 18.3 km (mean = 4.1 km; D.J. Green, unpublished data). Natal dispersal distances of up to 31 and 75 km have been documented in Oregon and Colorado, respectively (Kingery 1996, Price and Bock 1983).

Monitoring of breeding and territory departure

From 2003 to 2005, breeding pairs were monitored at least twice weekly from nest initiation (late February) to independence of the final brood (mid-July). Nests were visited at 10–14 days after hatching and each nestling was marked with a unique combination of three Darvic® colour bands and one aluminum US Fish and Wildlife Service band. Nestlings were weighed and measured at the time of banding. Mass was measured to 0.25 g using a Pesola spring balance, tarsus to 0.1 mm using calipers, and wing to 1 mm using a wing ruler. Daily visits were made to breeding territories when nestlings were 22 days old until the brood fledged to determine (*i*) the exact fledging dates and (*ii*) the total number of fledged young. The fledge date (day 1) was the day when the majority of the brood left the nest. We subsequently monitored fledglings each day until day 5 and then every 2–3 days until all young had disappeared or until day 14. We attempted to locate fledglings by searching the territory on foot, following adults, and listening for begging calls. Territories were searched by two observers until all brood members were resighted or 2 h had elapsed. The departure date of an individual was estimated as the midpoint between the last resighting and the subsequent visit to the territory. Fledglings that remained in their natal territory on day 14 were considered to have delayed dispersal. We used day 14 as a cut-off because fledglings that remain in their natal territory become increasingly hard to detect after this point since they are no longer provisioned by their parents or are fed at a much reduced rate (Middleton 2006).

Nestling sex, nestling condition, and postfledging behaviour

Fledgling sex was determined using a DNA-based test employing polymerase chain reaction amplification of a section the avian CHD1 genes (CHD1-W and CHD1-Z) located on the avian sex chromosomes (for details of the procedure see Griffiths et al. 1998). DNA was isolated from a blood sample (~25 μL) taken from the brachial vein of nestlings. Condition at banding was estimated using the residuals from a mass versus tarsus regression.

We conducted focal observations to determine parental provisioning rates and estimate the amount of time fledglings spent foraging independently during the first 5 days after nest departure. Fledglings were observed for up to an hour on any day that they were located (mean time observed over 5 days = 158 min, range = 55–297 min, N = 43). All observations were conducted between 1000 and 1400 to avoid any bias owing to temporal variation in foraging intensity and parental provisioning rates. Time budgets were calculated from instantaneous behavioural observations taken at 1 min intervals, where behaviour was categorized as foraging (pecking, head-dunking, diving, fly-catching), mobile (walking, wading, diving, flying), or stationary

(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 (proportion of 1 min samples spent foraging) and parental provisioning rates for this study were calculated using the combined sample.

Juvenile survival and local recruitment

Juveniles and migratory adults join sedentary adults on the main stem of the river during the nonbreeding season. Juvenile survival and local recruitment were evaluated using systematic censuses of the population conducted throughout the year and surveys of the watershed conducted during the breeding season. Population censuses were conducted at eight 2 km long locations on the main stem of the Chilliwack River in the first week of November, January, March, May, and July from 2003 to 2006 (for details see Gillis et al. 2008). Additional surveys, including 28 km on the main stem of the river and 17 km on tributary creeks, were conducted from March to July while searching for breeding pairs. Our censuses and surveys therefore included a large proportion of suitable breeding habitat on the main stem of the river but a relatively small proportion of suitable habitat at higher elevations. Juveniles were considered to have recruited locally if they were resighted in, or after, March in the year following birth.

Statistical analyses

We explored departure decisions and local recruitment using a mixed modelling approach, since broods consisted of multiple individuals and pairs produced up to two broods per year. Initial mixed models specified both pair and brood identities as random factors. However, there was little variance associated with the brood term (the standard errors of the variance component were large compared with the mean), so this term was dropped to simplify the analysis. We fitted separate generalized linear models to four dependant variables: survival to day 5 after nest departure (yes/no), dispersal within 14 days (yes/no) for individuals that survived to day 5, the timing of departure for those individuals that left their natal territory within 2 weeks, and local recruitment (yes/no). Binomial response data were modelled using a logit link function. We used a total of 11 explanatory variables in our models: the location ("river territory" occupied by residents or "creek territory" occupied by migrants), the social environment (the number of siblings), 2 temporal variables (year and fledge date), 4 attributes of the individual (sex, tarsus size at day 12, condition as a nestling, age at fledging), and 3 behavioural variables (foraging score, parental provisioning rate, and whether individuals dispersed within 14 days). We initially fitted models that included the location, number of siblings, two temporal variables, and the four variables that described individuals, as they were available for almost all fledglings ($N = 95$–102). A final model was selected by progressively eliminating nonsignificant terms ($P > 0.05$) until only significant terms remained. Significance of terms was assessed using the change in deviance when the term of interest was dropped from the model. We subsequently evaluated whether the behavioural variables explained any additional variation in departure or local recruitment. These data were available

for a subset of the fledglings that survived to day 5 (foraging and provisioning, $N = 43$; dispersal within 14 days, $N = 67$). All models were fitted using Genstat version 9.1 for Windows (VSN International Ltd., Hemel Hempstead, UK). When appropriate, model residuals were examined to ensure that the models conformed to assumptions of normality and heterogeneity of variances. Values reported refer to means ± SE.

Results

We monitored, on average, 23 pairs per year (year 2003 = 29 pairs, year 2004 = 15 pairs, year 2005 = 24 pairs). These pairs fledged up to two broods each year containing 2–5 young per brood. Nestlings left the nest approximately 25 days after hatching (25.0 ± 0.19 days, range = 22–31 days, $N = 99$). A total of 150 fledglings were produced over the course of this study. We monitored the timing of departure of 102 marked individuals (61 males and 41 females) from 30 broods.

General patterns

Twenty fledglings ($N = 102$) disappeared from their natal territory in the first 5 days after fledging. These individuals were assumed to have died since individuals disappearing during this period were never resighted. Fifteen fledglings from eight broods were not monitored between days 9 and 14, as we were unable to revisit these territories for logistical reasons. An additional 38 were last seen in their natal territory 6–13 days after nest departure. These were assumed to have dispersed, since young last observed 6 days after nest departure were occasionally resighted outside their natal territory at a later date and the daily mortality of fledglings was low, declining from 6% ($N = 102$) on the 1st day after fledging to 3.5% ($N = 85$) on the 5th day. Twenty-nine fledglings were known to be present in their natal territory 14 days after nest departure.
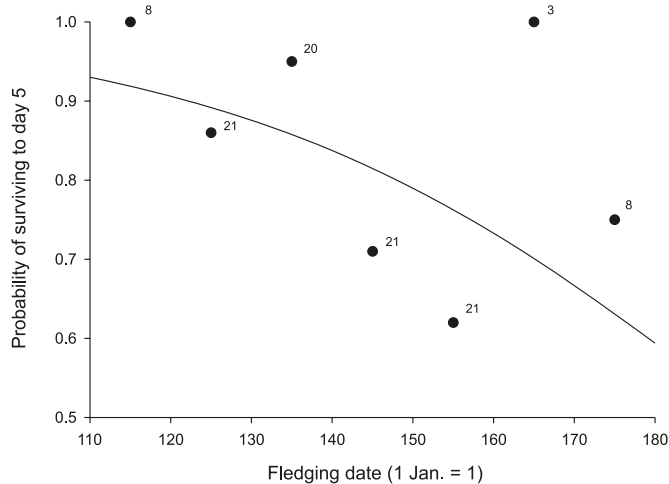
Postfledging survival

Male and female fledglings were equally likely to survive to day 5 after nest departure (predicted value ± SE — males: 0.84 ± 0.05; females: 0.81 ± 0.06; $\chi^2_{[1]} = 0.2$, $P = 0.65$). However, individuals that fledged early in the season ($\chi^2_{[1]} = 4.88$, $P = 0.03$; Fig. 1) and those fledging at an older age ($\chi^2_{[1]} = 4.44$, $P = 0.04$) were more likely to survive to day 5 than those that fledged later and at younger ages. The size or condition of an individual, measured as a nestling, did not have a significant effect on survival to day 5 (nestling size: $\chi^2_{[1]} = 2.60$, $P = 0.12$; nestling condition: $\chi^2_{[1]} = 2.45$, $P = 0.11$). The probability of survival to day 5 did not vary between years or differ depending on whether territories were located on the main stem of the river or on creek tributaries (year: $\chi^2_{[2]} = 1.20$, $P = 0.55$; territory location: $\chi^2_{[1]} = 0.04$, $P = 0.85$).

Causes of variation in timing of departure

Fifty-four percentage of the monitored fledglings that survived to day 5 had dispersed by day 14. Females were more likely to have dispersed than males (females: 20/28; males: 18/39; sex effect: $\chi^2_{[1]} = 4.12$, $P = 0.04$). No other attributes of individuals influenced whether fledglings had dispersed

Fig. 1. Relationship between fledging date and the probability American Dippers (*Cinclus mexicanus*) survive at least 5 days after leaving the nest. The line shows the prediction from the mixed model after controlling for the age at which juveniles fledge. The dots show the proportion that survived with the data points binned into 10-day categories. The numbers beside the dots show the sample size of each category.
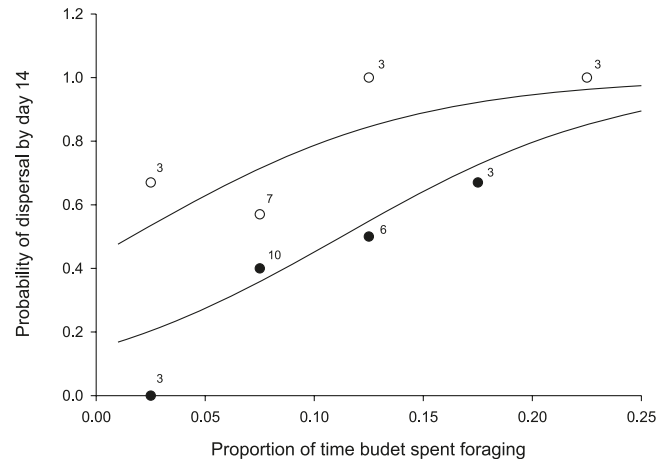

Fig. 2. Relationship between the proportion of time a juvenile American Dipper (*Cinclus mexicanus*) spends foraging in the first 5 days after fledging and the probability that they have dispersed by day 14. Lines show the model predictions for males (lower) and females (upper). The dots show the proportion of males (●) and females (○) that have dispersed with the data points binned into 0.05-unit categories. The numbers beside the dots show the sample size of each category.

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 × 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 ± 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

Although dispersal behaviour varies in many species, relatively few studies have examined what factors influence the timing of dispersal in species where individuals are obliged to disperse. We found that males and individuals that spent

Fig. 3. Relationship between the timing of dispersal in American Dippers (*Cinclus mexicanus*) and the probability that they survive to recruitment age.
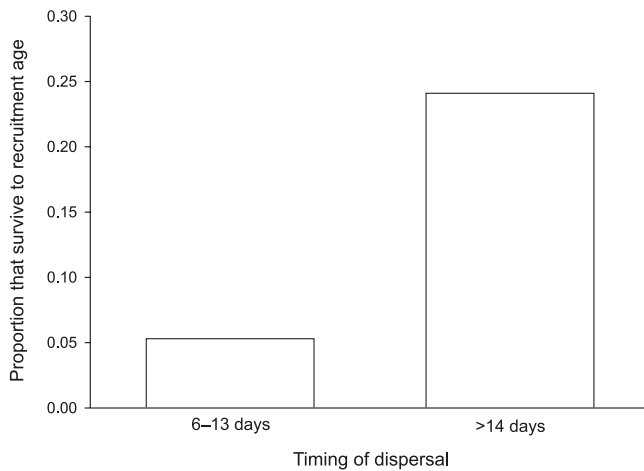
less time foraging were less likely to have dispersed within 14 days of fledging than females and individuals that foraged more. For juvenile American Dippers that did disperse within 14 days, those that fledged early in the season and at an older age spent less time in their natal territory. In contrast, 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 study that juvenile American Dippers are likely to obtain a significant fitness benefit from extending the amount of time they spend in their natal territory.

What influences postfledging survival to dispersal age?

Seasonal declines in juvenile survival have been documented in many bird species (e.g., Lack 1968; Hatchwell 1991; Spear and Nur 1994). This pattern is often attributed to older, experienced adults initiating breeding attempts earlier in the season than younger inexperienced breeders. In this study, American Dippers that fledged earlier in the season were more likely to survive the first 5 days after nest departure than young fledging later. Although we did not age breeding birds, previously banded birds initiated breeding earlier in the season than unbanded birds that moved into the study area, suggesting that parental age or experience may explain seasonal declines in juvenile survival in American Dippers. Seasonal effects on juvenile survival in American Dippers may arise because early (older) breeders occupy superior territories that have refuges from turbulent water or predators, or because early (older) breeders are more adept at moving young to safe areas or deterring predators. Seasonal effects appear less likely to arise because early breeders feed young more since nestling condition, considered alone or after controlling for fledging date, did not influence juvenile survival.

What influences the dispersal decisions of juvenile American Dippers?

Sex differences in the timing of dispersal have been documented in a variety of nonsocial bird species (e.g., Dhondt 1979; Alonso et al. 1998; Green and Cockburn 2001). We found that female American Dippers were almost twice as likely as males to have left their natal territory within 14 days of nest departure. This pattern may reflect sex differences in the benefits associated with extended natal philopatry when one sex does not disperse as far as the other. This argument is supported by data on at least three species where females disperse both earlier and farther than males (e.g., Great Tits, *Parus major* L., 1758 — Dhondt 1979; Brown Thornbills — Green and Cockburn 2001; Northern Goshawks, *Accipiter gentilis* (L., 1758) — Kenward et al. 1993) and one species where males disperse earlier and farther than females (Great Bustard, *Otis tarda* L., 1758 — Alonso et al. 1998). The proximate cause of sex differences in the timing of dispersal are less clear, but there was no indication that females were forced to leave earlier owing to competitive interactions with male siblings.

We found that male and female American Dippers that spent more time foraging independently early in the post-fledging period were more likely to have dispersed within 14 days of leaving the nest. These individuals foraged primarily on small prey found on the river bank (predominantly simuliid larvae) rather than on submerged invertebrates that are captured by head-dunking or diving (Middleton 2006). Similarly, Yoerg (1998) found that juvenile White-throated Dippers (*Cinclus cinclus* (L., 1758)) that spent more time foraging on small stationary prey and had higher intake rates became independent sooner, and Alonso et al. (1998) showed that juvenile male Great Bustards that fed at higher rates reached independence and initiated dispersal earlier. Alonso et al. (1998) argued that this pattern is predicted if individuals have to attain a threshold body mass to disperse. However, if the attainment of a threshold mass or body condition acted as an ontogenetic switch for dispersal, we might also have expected the condition of an individual as a nestling, the age at which they fledge, and the parental provisioning rate to influence whether an individual was able to disperse within 14 days of nest departure.

The relationship between the foraging behaviour and dispersal of juvenile American Dippers is also consistent with recent work that links the behavioural phenotype or personality of juvenile Great Tits to their dispersal behaviour (Dingemanse et al. 2003). Studies show that Great Tits with "fast" phenotypes explore a novel environment faster (Verbeek et al. 1994), are bolder (Verbeek et al. 1994), are more aggressive to conspecifics (Verbeek et al. 1996), are less flexible foragers (Drent and Marchetti 1999), and disperse farther than individuals with "slow" phenotypes (Dingemanse et al. 2003). Furthermore, selection experiments have demonstrated that these correlated traits are heritable (Drent et al. 2003). We currently have insufficient data to evaluate consistency in individual foraging behaviour, but believe that further work examining the relationship between social behaviour, foraging behaviour, and dispersal strategies in American Dippers is warranted.

Consequences of variation in the timing of dispersal

Recent studies suggest that delayed dispersal can benefit juveniles of species that do not breed cooperatively. For example, in the socially monogamous Brown Thornbill, males that delayed dispersal had higher survival and were

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.

References

Alonso, J.C., Martin, E., Alonso, J.A., and Morales, M.B. 1998. Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. Behav. Ecol. **9**: 243–352. doi:10.1093/beheco/9.3.243.

Clarke, A.L., Sæther, B.E., and Røskaft, E. 1997. Sex biases in avian dispersal — a reappraisal. Oikos, **79**: 429–438. doi:10.2307/3546885.

Cockburn, A., Osmond, H.L., Mulder, R.A., Green, D.J., and Double, M.C. 2003. Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren *Malurus cyaneus*. J. Anim. Ecol. **72**: 189–202. doi:10.1046/j.1365-2656.2003.00694.x.

Cody, M.L. (*Editor*). 1985. Habitat selection in Birds. Academic Press, London, UK.

Currie, D., and Matthysen, E. 1998. Nuthatches Sitta europaea do not delay postfledging dispersal in isolated forest fragments. Belg. J. Zool. **128**: 49–54.

Dhondt, A.A. 1979. Summer dispersal and survival of juvenile Great tits in Southern Sweden. Oecologia (Berl.), **42**: 139–157. doi:10.1007/BF00344854.

Dingemanse, N.J., Both, C., Van Noordwijk, A.J., Rutten, A.L., and Drent, P.J. 2003. Natal dispersal and personalities in great tits (*Parus major*). Proc. R. Soc. Lond. B Biol. Sci. **270**: 741–747. doi:10.1098/rspb.2002.2300.

Doligez, B., Danchin, É., and Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. Science (Washington, D.C.), **297**: 1168–1170. doi:10.1126/science.1072838. PMID:12183627.

Drent, P.J., and Marchetti, C. 1999. Individuality, exploration and foraging in hand raised juvenile great tits. *In* Proceedings of the 22nd International Ornithological Congress, Durban, South Africa, 1998. Birdlife South Africa, Johannesburg.

Drent, P.J., van Oers, K., and van Nordwijk, A.J. 2003. Realized heritability of personalities in the great tit. Proc. R. Soc. Lond. B Biol. Sci. **270**: 45–51. doi:10.1098/rspb.2002.2168.

Ekman, J.B., Bylin, A., and Tegelstrom, H. 1999. Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. Proc. R. Soc. Lond. B Biol. Sci. **266**: 911–915. doi:10.1098/rspb.1999.0723.

Ekman, J.B., Eggers, S., and Griesser, M. 2002. Fighting to stay: the role of sibling rivalry for delayed dispersal. Anim. Behav. **64**: 453–459. doi:10.1006/anbe.2002.3075.

Ellsworth, E.A., and Belthoff, J.R. 1999. Effects of social status on the dispersal behavior of juvenile Western Screech Owls. Anim. Behav. **57**: 883–892. doi:10.1006/anbe.1998.1050. PMID:10202096.

Gillis, E.A., Green, D.J., Middleton, H.A., and Morrissey, C.A. 2008. Life history correlates of alternative migratory strategies in American Dippers. Ecology, **89**: 1687–1695. doi:10.1890/07-1122.1.

Green, D.J., and Cockburn, A. 2001. Post-fledging care, philopatry and recruitment in Brown Thornbills. J. Anim. Ecol. **70**: 505–514. doi:10.1046/j.1365-2656.2001.00503.x.

Greenwood, P.J., and Harvey, P.H. 1982. The natal and breeding dispersal of birds. Annu. Rev. Ecol. Syst. **13**: 1–21. doi:10.1146/annurev.es.13.110182.000245.

Griffiths, R., Double, M.C., Orr, K., and Dawson, R.J.G. 1998. A DNA test to sex most birds. Mol. Ecol. **7**: 1071–1075. doi:10.1046/j.1365-294x.1998.00389.x. PMID:9711866.

Hatchwell, B.J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of common guillemots (*Uria aalge*). J. Anim. Ecol. **60**: 721–736. doi:10.2307/5410.

Heinsohn, R.G. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. Am. Nat. **137**: 864–888. doi:10.1086/285198.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk, **118**: 557–562. doi:10.1642/0004-8038(2001)118[0557:HSSIAE]2.0.CO;2.

Kenward, R.E., Marcstrom, V., and Karlbom, M. 1993. Post-nestling behaviour in goshawks *Accipiter gentiles*. I. The causes of dispersal. Anim. Behav. **46**: 365–370. doi:10.1006/anbe.1993.1198.

Kingery, H.E. 1996. American Dipper (*Cinclus mexicanus*), The birds of North America [online]. *Edited by* A. Poole. Cornell Laboratory of Ornithology, Ithaca, N.Y. Available from http://bna.birds.cornell.edu/bna/species/229/articles/introduction.

Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L., and Stanback, M.T. 1992. The evolution of delayed dispersal in cooperative breeders. Q. Rev. Biol. **67**: 111–150. doi:10.1086/417552. PMID:1635976.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen Press, London.

Lens, L., and Dhondt, A. 1994. Effects of habitat fragmentation on the timing of crested tit *Parus cristatus* natal dispersal. Ibis, **136**: 147–152. doi:10.1111/j.1474-919X.1994.tb01078.x.

Middleton, H.A. 2006. Post-fledging behaviour and dispersal in American dippers. M.Sc. thesis, Simon Fraser University, Burnaby, B.C.

Morrissey, C.A. 2004. Effect of altitudinal migration within a watershed on the reproductive success of American Dippers. Can. J. Zool. **82**: 800–807. doi:10.1139/z04-042.

Mulder, R.A. 1995. Natal and breeding dispersal in a cooperative, extra-group-mating bird. J. Avian Biol. **26**: 234–240. doi:10.2307/3677324.

Newton, I., and Marquiss, M. 1983. Dispersal in sparrowhawks between birthplace and breeding place. J. Anim. Ecol. **52**: 463–477. doi:10.2307/4566.

Nilsson, J.-A. 1989. Causes and consequences of natal dispersal in the Marsh Tit, *Parus palustris*. J. Anim. Ecol. **58**: 619–636. doi:10.2307/4852.

Nilsson, J.-A., and Smith, H.G. 1985. Early fledgling mortality and the timing of juvenile dispersal in the Marsh Tit *Parus palustris*. Ornis Scand. **16**: 293–298. doi:10.2307/3676693.

Nilsson, J.-A., and Smith, H.G. 1988. Effects of dispersal date on winter flock establishment and social dominance in marsh tit *Parus palustris*. J. Anim. Ecol. **57**: 917–928. doi:10.2307/5101.

Price, F.E., and Bock, C.E. 1983. Population ecology of the dipper (*Cinclus mexicanus*) in the Front Range of Colorado. Stud. Avian Biol. **7**: 1–84.

Spear, L., and Nur, N. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. J. Anim. Ecol. **63**: 283–298. doi:10.2307/5547.

Strickland, D. 1991. Juvenile dispersal in Gray Jays: dominant brood member expels siblings from natal territory. Can. J. Zool. **69**: 2935–2945. doi:10.1139/z91-414.

Verbeek, M.E.M., Drent, P.J., de Jong, G., and Wiepkema, P.R. 1994. Consistent individual differences in the early exploratory behaviour of male great tits. Anim. Behav. **48**: 1113–1121. doi:10.1006/anbe.1994.1344.

Verbeek, M.E.M., Boon, A., and Drent, P.J. 1996. Exploration, aggressive behaviour and dominance in pairwise confrontations of juvenile male great tits. Behaviour, **133**: 945–963. doi:10.1163/156853996X00314.

Verboven, N., and Visser, M.E. 1998. Seasonal variation in local recruitment of great tits: the importance of being early. Oikos, **81**: 511–524. doi:10.2307/3546771.

Wiens, J.D., Reynolds, R.T., and Noon, B.R. 2006. Juvenile movement and natal dispersal of Northern Goshawks in Arizona. Condor, **108**: 253–269. doi:10.1650/0010-5422(2006)108[253:JMANDO]2.0.CO;2.

Yoerg, S.I. 1998. Foraging behavior predicts age at independence in juvenile Eurasian Dippers (*Cinclus cinclus*). Behav. Ecol. **9**: 471–477. doi:10.1093/beheco/9.5.471.