POST-FLEDGING BEHAVIOUR AND DISPERSAL IN AMERICAN DIPPERS

by

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ABSTRACT

The post-fledging period is a critical stage in the avian life cycle since foraging skill development and dispersal decisions are known to influence survival and reproductive success. I studied parental care, begging patterns and natal dispersal decisions in fledgling American dippers (*Cinclus mexicanus*). In contrast to studies of nestlings, begging by fledglings varied with interannual variation in parental provisioning rates but not hunger levels. Parents initially allocated food preferentially to the fledgling begging at the highest intensity and the closest proximity but did not respond to variation in begging intensity as fledglings approached independence age. Dispersal varied with females, on average, leaving before males. Males that delayed dispersal beyond 12-14 days increased their likelihood of surviving to recruitment age and gaining a local breeding vacancy.

Keywords: American dipper, post-fledging period, foraging skill development, natal dispersal, begging, parental care

DEDICATION

to my parents, who encouraged and nurtured my sense of individuality and, to this day, lend support to my every dream

ACKNOWLEDGEMENTS

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CHAPTER ONE: INTRODUCTION

The post-fledging period is a critical period in the avian life cycle. Fledgling mortality rates are higher than any other life stage. An extensive review found that 42-86% of fledgling birds die before they reach independence and juvenile survival rates are typically half that of adults (Newton 1989). Consequently, factors that influence juvenile survival from fledging to breeding age play an important role in determining the lifetime reproductive success of adults (Newton 1998). Fledgling survival has been found to be influenced by parental age or experience (Green 2001), condition as a nestling or fledgling (Heinsohn 1991, Donnelly and Sullivan 1998, Magrath 1991) and fledgling foraging proficiency (Sullivan 1988, Donnelly and Sullivan 1998, Leary et al. 1999). Fledgling condition, which is influenced by parental provisioning rates and its own foraging efficiency, also has affects on the timing of nutritional independence (Davies 1976) and departure decisions (Ellworth and Belthoff 1999).

Decisions about when to reach independence and depart the natal territory impact subsequent life events. Survival, dominance status in winter flocks, the quality of breeding territory acquired and subsequent reproductive success are all impacted by when a fledgling departs its natal territory (Drent 1984, Ekman and Askenmo 1984, Eden 1987, Nilsson and Smith 1988, Ekman and Rosander 1992, Ekman et al. 1999, Lens and Dhondt 1994). This suggests that development patterns and behavioural decisions made during the post-fledging period impact individuals over the short and long term.

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However, studies examining parental care, foraging skill development and dispersal decisions of fledglings are limited (but see Davies 1976, Sasvári 1990, Smith et al. 2005, Wunderle 1991, Ekman et al. 2002, Baglione et al. 2006).

Study species and study system

American dippers (*Cinclus mexicanus*) are obligate aquatic passerines that inhabit fast-flowing mountain rivers and streams across western North America. They are morphological adapted to an aquatic environment with an enlarged preen gland, additional layers of feathers, a nictitating membrane on the eye and heat-exchange system in their legs. While foraging underwater they use their feet to cling to the substrate and propel themselves through the water by beating their wings. Dippers are visual hunters preying on aquatic invertebrate larvae, emerged aerial insects and salmon fry and eggs using a wide range of foraging behaviours. Adults forage by pecking at prey on the riverbank, head dunking, wading, swimming and diving for prey submerged in the water and by catching aerial insects on the wing.

Dippers are an ideal avian system for examining post-fledging behaviour because they occupy linear, two-dimensional territories that allows individuals to be easily located and observed. The fledgling dependent period is relatively short (6 days to 3 weeks, Kingery 1996) in comparison with other passerine species permitting study of the post-fledging period over a short span of time. They exhibit bi-parental care and are often double brooded allowing us to examine the roles of brood order and timing of the brood in the season on provisioning patterns and departure decisions (Kingery 1996). Finally, adult dippers use a suite of discrete foraging behaviours that are known to vary in

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energetic cost (Bryant and Tatner 1988) making them ideally suited to examination of development of foraging behaviour during the transition to independence.

This study was conducted within the Chilliwack River watershed. The watershed is located approximately 150km east of Vancouver, British Columbia, in the Coast Mountain range (Figure 1). The watershed is fed from the east by Chilliwack Lake, consists of first- through fourth-order streams and drains an area of 1,200km^2. This study was conducted on 16km of the main stretch of the river and a total of about 10km on the 5 largest tributaries (Liumchen, Tamihi, Borden, Slesse and Foley Creeks). The watershed supports the largest dipper population in the Lower Mainland (Morrissey et al. 2004) and high biological diversity (fraser valley watershed coalition: www.fvrwc.org/chilliwackriver.html). Population-wide censuses of marked individuals that aggregate on the low-lying river in winter allows assessment of juvenile survival rates.

The Chilliwack River population has been the subject of an ongoing study initiated in 1999 by C. A. Morrissey (Morrissey 2002). Morrissey (2002) demonstrated that this population consists of both migratory individuals that move between breeding territories on high-elevation creeks and the low elevation wintering area and sedentary individuals (residents) that hold multi-purpose territories on the main stem of the river throughout the year. The movement of migrants to higher elevation was found to delay the initiation of breeding by approximately 2 weeks and, as a result, migrants produced fewer young and fewer second broods than did residents (Morrissey 2004). Breeding territories occupied by migrants and residents also differed in habitat structure, water flow and prey availability (Morrissey 2004). Stable isotope analysis demonstrated that

migrants had a lower proportion of fish in their diet during the breeding season than residents (migrants: 22%± 6%, residents: 42%± 7%). Although food type and availability may differ, the presence of both migratory and sedentary pairs within the watershed makes this system ideal for examining the effects of strategy-related differences in food availability and habitat structure on provisioning patterns, begging, skill development, timing of natal departure and fledgling survival to breeding age.

Focus of thesis

In this thesis I examine patterns of food acquisition, changes in foraging behaviour and timing of natal territory departure during the post-fledging period in American dippers. Chapter Two focuses on the information content of fledgling begging and the use of begging in allocation decisions by provisioning parents. Chapter Three explores patterns of foraging skill development from nest departure to natal territory departure. In the fourth chapter I address the causes of variation in timing of natal territory departure. Finally, I summarize the findings of this study and make suggestions for further research in light of my results.
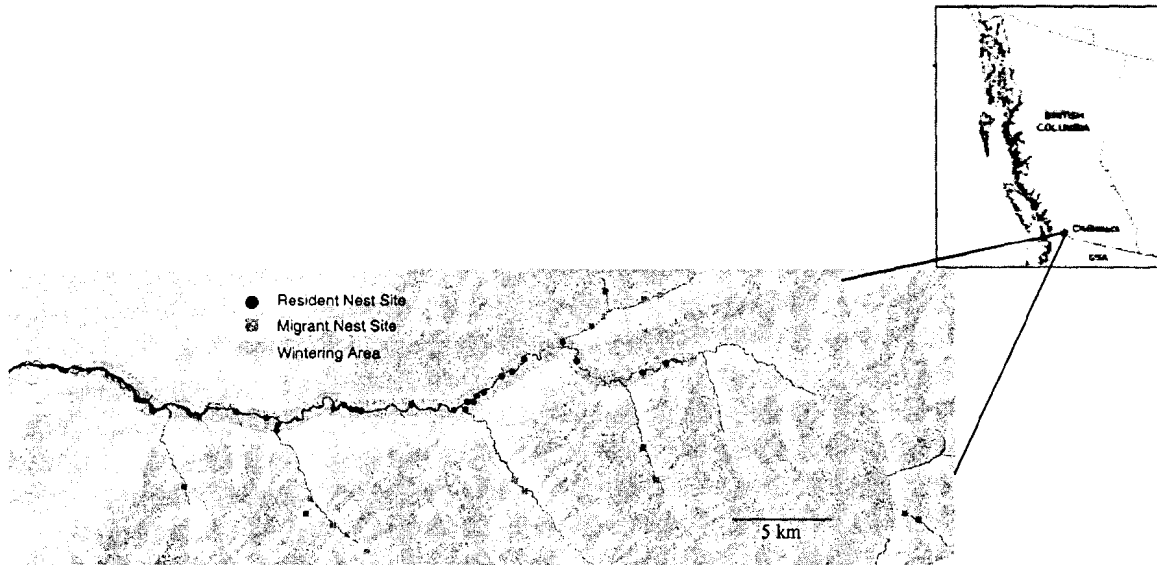
Figure 1 Map of Chilliwack River watershed in southwestern British Columbia.

CHAPTER TWO: FLEDGLING BEGGING AND PARENTAL RESPONSIVENESS IN AMERICAN DIPPERS (*CINCLUS MEXICANUS*).

Introduction

Young birds solicit resources from parents using conspicuous begging signals. Observational and experimental studies have shown a strong link between nestling begging and immediate hunger (Bengtsson and Ryden 1983, Smith and Montgomerie 1991, Redondo and Castro 1992a, Price and Ydenberg 1995). For example, signal intensity increases when nestlings are deprived of food (Bengtsson and Ryden 1983, Smith and Montgomerie 1991) and decreases when nestlings are satiated (Bengtsson and Ryden 1983, Redondo and Castro 1992a). In nestlings, the correlation between hunger and signal intensity is argued to be maintained via energetic and predation costs (Godfray 1995, Redondo and Castro 1992b, Haskell 1994).

In addition to reflecting short-term hunger, begging could also reflect long-term patterns of food distribution and consequently function to communicate a chick's condition (Price et al. 1996, Iacovides 1998, Sacchi et al. 2002). Early observational studies suggested that begging may express long-term need (Ryden and Bengtsson 1980, Stamps et al. 1989). For example, in budgerigars (*Melopsittacus undulatus*), begging intensity was higher in last-hatched young, who received greater marginal benefit from a food item than older siblings (Stamps et al. 1989). However, few studies have experimentally demonstrated the contribution of long-term need to nestling begging

(Price et al. 1996, Iacovides 1998). In fledglings, condition can influence subsequent survival (e.g. Heinsohn 1991) so begging may signal condition more frequently in fledglings.

Begging intensity can also be influenced by sibling competition. Begging is predicted to escalate when brood size increases (Leonard et al. 2000) and nestlings vary in competitive ability (Leonard et al. 2000, Krebs 2001, Neuenschwander et al. 2003) or relatedness (Briskie et al. 1994). In nestling tree swallows (*Tachycineta bicolor*), individual begging intensity escalated as brood size increased (Leonard et al. 2000). However, most studies examine begging of young confined to the nest, yet free-moving fledglings can actively avoid or promote sibling competition. Sibling competition could potentially play a more important role in begging behaviour of fledglings.

Begging intensity is frequently used by adult birds when allocating food in the nest. In most species, parents preferentially feed the nestling begging most conspicuously; ie the closest, loudest and/or largest nestling relative to nestmates (Redondo and Castro 1992a, Kilner 1995, Leonard and Horn 1996, Price et al. 1996, Kolliker et al. 1998). Parents will benefit from this allocation pattern if begging is an honest reflection of need, allowing food to be directed to the nestling that will benefit most from care (Godfray 1991, 1995).

As fledglings become older, parents and offspring may be in conflict over the timing of independence (Trivers 1974). Although fledgling begging should decrease with age and improved foraging efficiency (Moreno 1984, Langen 1996), parents may also become less responsive to begging as fledglings age. Accordingly, parents should increase the return time to fledglings and/or disregard variation in begging intensity

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(Davies 1976). Further understanding of how provisioning rules change during the transition to independence would provide insight into parent-offspring conflict.

In order to understand begging strategies and parental allocation patterns during the post-fledging period I examined the behaviour of parents and fledglings during the 2-week fledgling dependant period in American dippers (*Cinclus mexicanus*). Dippers are well-suited to the study of post-fledging behaviour because the linear, two-dimensional territory permits parent-offspring interactions to be clearly monitored. Specifically I asked (1) whether begging reflects short-term or long-term need (2), what social and intrinsic factors influence begging (3), whether, in the post-fledging period, parents use begging to make provisioning decisions and 4) whether parental responses to begging change at the approach of independence.

Methods

Study species and study area

I studied American dippers in the Chilliwack River watershed in southwestern British Columbia (49° 02'N and 121 °04'W). The 43.5 km long Chilliwack River is a fourth order stream fed by Chilliwack Lake to the east and seven tributaries. The watershed ranges from 50 to 2,500 m in elevation and drains an area of 1,200 km^2. Breeding birds were monitored at six sites along the main stem of the Chilliwack River and on four tributaries. The six river sites were each approximately 2 km long separated by 4-5 km of unmonitored stream, while accessible sections of each tributary ranged from 1 to 3 km in length. Additional details of the study area are provided in Morrissey (2004).

American dippers (*Cinclus mexicanus*) are obligate aquatic passerines that rely on fast-flowing mountain streams for wintering and breeding. Females lay 1-2 clutches containing 3-5 eggs. Females incubate and brood the nestlings but both parents contribute to provisioning of nestlings and fledglings (Kingery 1996). My study population is composed of both resident and migratory individuals. Migrants move between breeding territories on higher elevation tributaries and wintering areas on the main stem of the Chilliwack River. Residents hold year-round multi-purpose territories on the main stem of the river. Migration delays the onset of breeding by 1-2 weeks and as a consequence migrants are less likely to be double brooded and have lower reproductive success (Morrissey 2004, Gillis et al. submitted).

Monitoring of breeding

The study was conducted from late February until mid-July of 2003-2005. Breeding adults were captured in mist nets and marked with a unique combination of three darvic colour bands and one USFWS aluminum band. All pairs were monitored throughout the breeding season from nest initiation (nest building) until fledging (24-26 days after hatching). Ten to 14 days after hatching nestlings were banded and weighed to the nearest 0.25g using a spring balance. Territories were visited on a daily basis preceding the predicted fledge date (24-26 days after hatching) to determine the fledge date and the number of nestlings that fledged.

Molecular sex determination

At the time of nestling banding a blood sample (~25μL) was collected from the brachial vein. DNA was later extracted from the blood samples using a standard

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ammonium salt extraction. I determined fledgling sex using a DNA-based test employing PCR amplification of a section the avian CHD1 genes (CHD1-W and CHD1-Z) located on the avian sex chromosomes (Griffiths et al. 1998).

Focal Observations

In 2003-2005 I attempted to make detailed observations on all brood members at 8 ages, the first five days after nest departure and three times between 6-8, 9-11 and 12-14 days after nest departure. On average, individuals were observed 4 times. Sample sizes of each age varied as not all individuals could be located on each day and some fledglings died or left their natal territory before 14 days. Focal fledglings were observed for approximately one hour on each observation day (mean: 56 min, range: 20-115 min). I recorded the number of food deliveries made by each parent, whether a fledgling was alone or close to a sibling, and the begging intensity of the focal fledgling each time it was approached with food. Begging intensity was recorded using a four-point scale: (0) no vocal or visual response; (1) either a vocal response or a wing-flutter; (2) a vocal response with wing flutter and/or crouching; and (3) loud, sustained vocal response, intense wing beating, crouching, gaping and facing the parent. When the focal fledgling was close (<5m) to a sibling I also recorded the begging score of the sibling. In 2005, I also recorded the position of the focal fledgling relative to its sibling when the parent landed on the riverbank (closest or furthest).

Statistical Analyses

I analyzed the data using a mixed modelling approach because my data included multiple observations on the same individual from broods containing 2-5 fledglings.

Provisioning and begging behaviour were initially explored by fitting mixed models to two dependant variables; total food delivery rate and mean begging intensity. Explanatory variables included year (2003-2005), fledge date, fledgling age, fledgling sex, whether the pair subsequently re-nested or not, brood size at observation age and the percent of time spent ≤5m from a sibling. I subsequently examined whether begging signals influenced 1) whether a focal fledgling was fed or not when parents chose between two siblings in close proximity and 2) the time taken to return to a focal fledgling with another food item. I predicted that parental responses to begging intensity would change as fledglings approached independence so, for the latter analysis, I examined data from week 1 and week 2 after nest departure separately. Explanatory variables included begging intensity (or relative begging intensity compared to a sibling), parental and fledgling sex, days since nest departure, fledge date and year.

Models examining continuous dependant variables were analyzed using the 'restricted maximum likelihood' (REML) procedure and dichotomous dependant variables were run using the Generalized Linear Mixed Model (GLMM) procedure using GENSTAT 5.4.1 for Windows (GENSTAT 5 Committee 1997). Initially all mixed models identified individual and brood as random factors. However, brood was subsequently dropped as there was little variance associated with the use of this random term (see Legge et al. 2001, for rationale). Initial models were fitted including all main effects and relevant interaction terms. Final models were selected by systematically eliminating all non-significant interaction terms and then main effects until only significant terms remained. To determine the significance of a variable, the deviance of the full model was compared to the deviance of the submodel containing the same

variables, but excluding the variable of interest. For continuous dependant variables, significance was determined using the Wald statistic associated with the change in deviance of a factor from the full model when it was the final factor in the model. The Wald statistic approximates a chi-square distribution (Payne 2006). I tested whether models conformed to the assumptions of normality and equal variances by examining residual and normal probability plots.

To examine how begging varied with short-term hunger I regressed chick begging intensity against the full range of time gaps between feeding events for each individual and tested whether these standardized regression coefficients were significantly different from a null of zero which represents no change in begging intensity in relation to inter-feed interval. I also compared the mean begging intensity of a solitary individual in the first five days following a long break between feeding events (>20minutes) and short break between feeding events (<4min) using a repeated measures ANOVA controlling for year.

Results

Interannual variation of dippers

Fewer pairs initiated breeding in 2004 than in 2003 or 2005. This resulted primarily from fewer migrant pairs attempting to breed. Pairs that did breed initiated breeding earlier in 2004 than 2003 and 2005 (after controlling for known differences in the timing of breeding by residents and migrants (Morrissey 2004)). Brood sizes did not differ between years. Breeding pairs in 2004, despite starting to breed sooner, were no

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more likely to initiate a second brood than breeding pairs in 2003 or 2005, and produced a similar number of fledglings over the season (Table 1).

Food delivery rates to individual fledglings

Total food delivery rate to fledglings was highest in 2005 and lowest in 2004 ($\chi^2 = 20.14$, df = 2, p = 0.001). Delivery rates increased until 5 days after nest departure and declined slightly in the second week ($\chi^2 = 14.75$, df = 7, p = 0.04; Figure 2). Male and female fledglings were fed at the same rate ($\chi^2 = 0.06$, df = 1, p = 0.80). Food delivery rate was not influenced by whether a pair attempted a subsequent nesting attempt ($\chi^2 = 0.91$, df = 1, p = 0.63), brood size ($\chi^2 = 4.4$, df = 4, p = 0.35) and the amount of time the focal individual was located within 5m of a sibling ($\chi^2 = 0.88$, df = 1, p = 0.35).

What factors influence fledgling begging intensity?

Fledglings typically begged only in the presence of an adult. Begging was not influenced by factors typically cited by previous begging studies. Mean begging intensity did not differ with the number of days since nest departure ($\chi^2 = 7.6$, df = 7, p = 0.37) or the sex of the fledgling ($\chi^2 = 0.48$, df = 1, p = 0.49). Fledging date did not influence mean begging intensity ($\chi^2 = 0.01$, df = 1, p = 0.92). Mean begging intensity also did not increase as the amount of time a fledgling was in close proximity to a sibling increased ($\chi^2 = 2.13$, df = 1, p = 0.14). Surprisingly, mean begging intensity was strongly influenced by year, even after controlling for other potential factors. Mean begging intensity was higher in 2004 compared to 2005 (Table 1) suggesting that begging was primarily influenced by inter-annual variation in delivery rates.

To investigate whether short-term hunger correlated to the intensity of begging, I examined whether regression coefficients from regressions relating the begging intensity of an individual to the time interval since the last food delivery differed from zero (mean standardized regression coefficient r = -0.01 ± 0.01, Figure 3a). I found that coefficients did not differ significantly from zero in either 2004 (mean r = -0.02, t = -1.34, p = 0.19) or 2005 (mean r = 0.02, t = 1.44, p = 0.18) suggesting that begging intensity was not influenced by time elapsed between feeding events.

Secondly, I examined how begging intensity changes when fledglings are relatively food-deprived versus satiated. An individual's begging intensity was not influenced by whether a short or long period of time preceded the delivery of a food item (time since last feed: $F_{1,38} = 0.29$, p = 0.59). Despite higher mean begging intensities in 2004, fledgling begging intensity was not greater after long gaps between feeding events than short gaps (repeated measures ANOVA: year effect: $F_{1,38} = 20.33$, p < 0.001, Figure 3b).

Parent provisioning rules

In the first week, male and female parents allocated food in the same way. Both males and females fed the fledgling begging at the highest intensity when given a choice between two fledglings (begging intensity effect: $\chi^2 = 51.2$, df = 1, p < 0.001, parent sex effect: $\chi^2 = 0.1$, df = 1, p > 0.1, parent sex by begging intensity interaction: $\chi^2 = 0.01$ df = 1, p= 0.92, Figure 4). In 2005, when more detailed data was collected on chick proximity, parents were also more likely to feed the fledgling that was closest to them when they landed on the riverbank (closest: 0.62±0.01, furthest: 0.35±0.04; $\chi^2 = 6.4$, df = 1, p = 0.011) but controlling for proximity did not alter the result that begging intensity

Table 1 Interannual variation (± SE) in breeding parameters and behaviour during the post-fledging period. Data control for known differences in breeding parameters between migrant and resident breeders. Data for begging intensity in 2003 were not available.

Variable	2003	2004	2005	Test statistic	P value
Number of breeding pairs (% migrants)	29 (31%)	15 (27%)	24 (39%)		
Clutch initiation date	April 7 ± 6 days	March 28 ± 10 days	April 13 ± 6 days	F_2: 4.28	0.02
Brood size	3.43 ± 0.56	3.25 ± 1.29	3.45 ± 0.65	χ^2: 0.68	NS
Proportion initiating a second clutch	0.3 ± 0.18	0.27 ± 0.25	0.14 ± 0.18	χ^2: 0.41	NS
Proportion fledging ≥1 young	0.70 ± 0.2	0.53 ± 0.27	0.61 ± 0.19	χ^2: 0.80	NS
Fledging success	2.65 ± 0.8	1.7 ± 1.11	1.93 ± 0.79	χ^2: 0.31	NS
Number of food deliveries per hour	7.89±2.25	5.48±0.66	13.51±1.36	χ^2_2: 12.04	NS
					<0.01
Average fledgling begging intensity		2.5±0.06	2.17±0.11	χ^2_1: 6.4	0.03
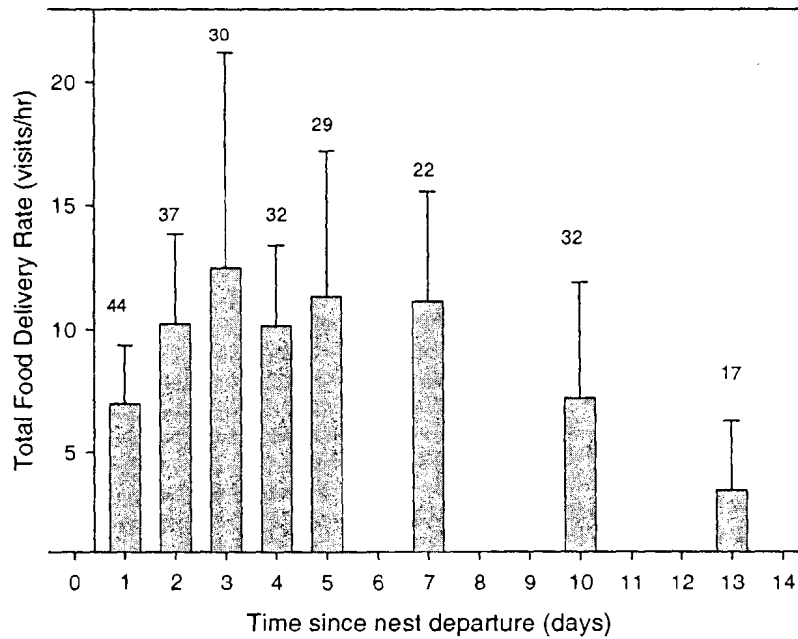
Figure 2 Relationship between the time since nest departure and total number of food items delivered to individual fledgling American dippers by both parents (2003-2005). The bars show the mean ($\pm$95% confidence intervals). Numbers above bars show number of fledglings observed at each time interval. Data are drawn from a total of 61 fledglings from 28 broods. Data were analysed after being $\log_{10}$ transformed but raw data are presented here for ease of interpretation.

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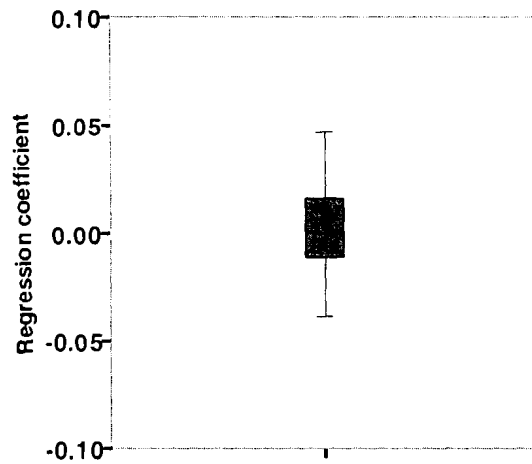
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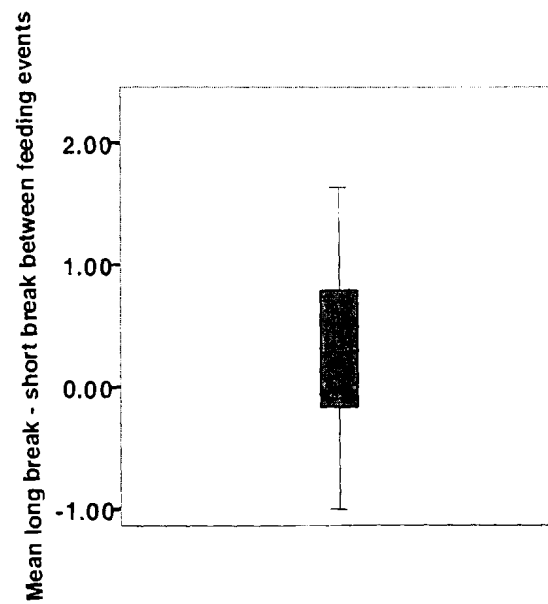
Figure 3 Box plots showing (A) regression coefficients for individual relationship between begging intensity and the time gaps since the last feeding event and (B) differences between mean begging intensities following short (<4min) and long (>20min) gaps between feeding events. The median is at the mid line, the box contains 50% of data and 95% of the data is bound by the whiskers. Data is drawn from a total of 46 individuals from 17 broods.

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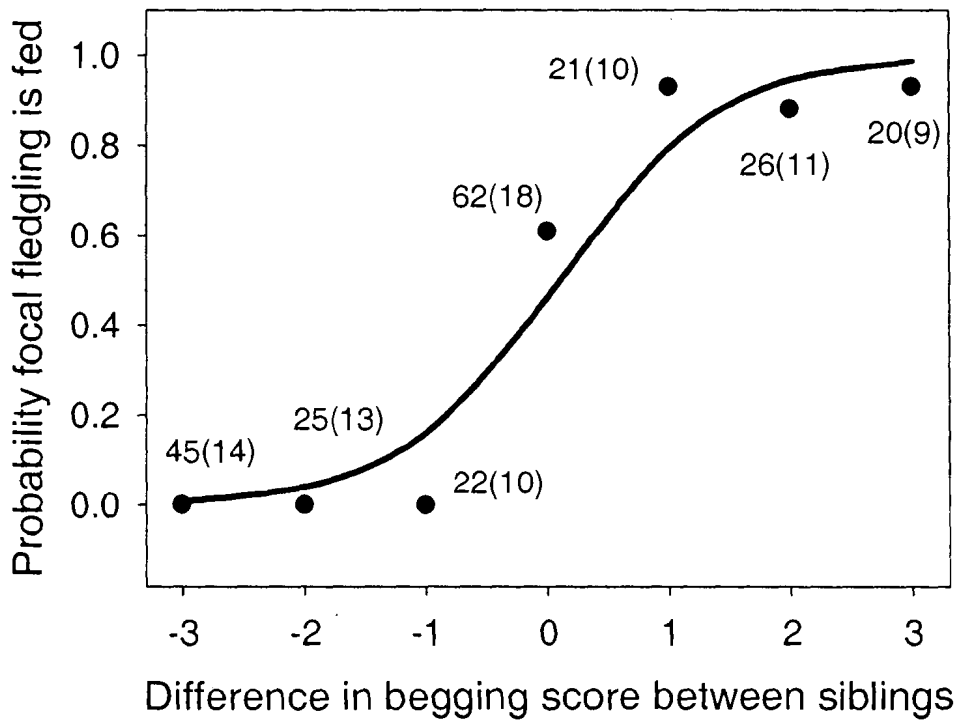
Figure 4 Relationship between the relative begging intensity of a fledgling compared to its nearby sibling and the probability of being fed. Positive values represent individuals begging at a higher intensity than its sibling. Negative numbers represent individuals begging at a lower intensity than its sibling. The curve shows the prediction from a mixed model. The numbers represent the number of observations (number of focal individuals) for each difference score. The data is drawn from a total of 37 individuals from 17 broods.

influenced provisioning decisions ($\chi^2 = 6.5$, df = 1, p = 0.011).

In the first five days post-fledging parents returned with food more quickly when fledglings begged more intensely (begging intensity effect: $\chi^2 = 7.9$, df = 2, p = 0.02, parent sex by begging intensity: $\chi^2 = 1.0$, df = 2, p = 0.61; Figure 5a) and did not differ in their response times ($\chi^2 = 0.1$, df = 1, p = 0.95, all interactions with parent sex: p > 0.1).The return time of both sexes tended to be longer in 2004 than in 2005 ($\chi^2 = 2.8$, df =1, p = 0.09). Return time also declined from fledging to day 5 ($\chi^2 = 13.5$, df = 4, p = 0.02).

In the second week after fledging, parents no longer responded to begging intensity by returning more quickly ($\chi^2 = 0.97$, df = 2, p = 0.81; Figure 5b). Parents generally took longer to return with food in the second week in 2005 than 2004 ($\chi^2 = 4.13$, df = 1, p = 0.04). Females took less time to return than males in week two but the two parents did not differ in how they responded to age, sex or begging behaviour of their fledglings (females: LS mean± SE= 1.43min ± 0.245, males: LS mean± SE= 3.42min ± 0.586; $\chi^2 = 4.92$, df = 1, p = 0.03) (parent sex by begging intensity: $\chi^2 = 1.1$, df = 5, NS).

Discussion

Studies of nestling begging show that begging reflects the hunger level of an individual such that individuals beg at higher intensities when they are deprived of food (Bengtsson and Ryden 1983, Smith and Montgomerie 1999). I found that fledgling dippers received more food when they begged more intensely. However, in contrast to previous studies, I found that begging by fledgling dippers did not reflect short-term

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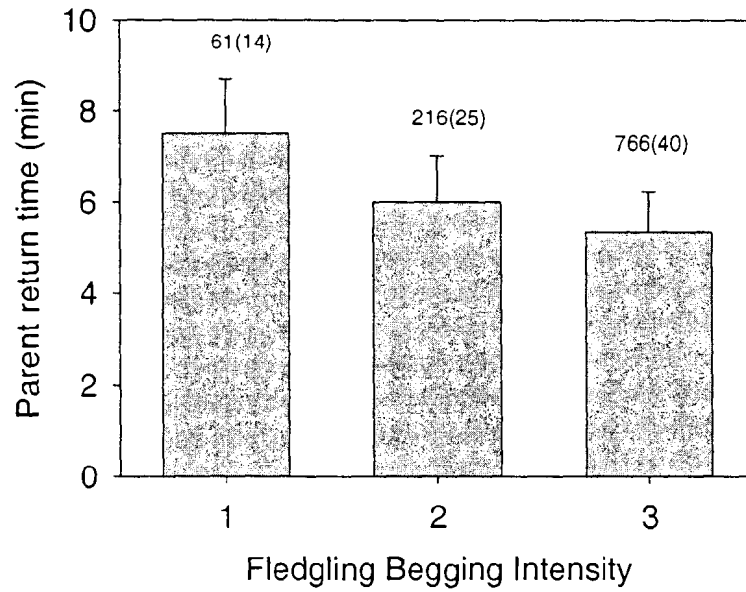
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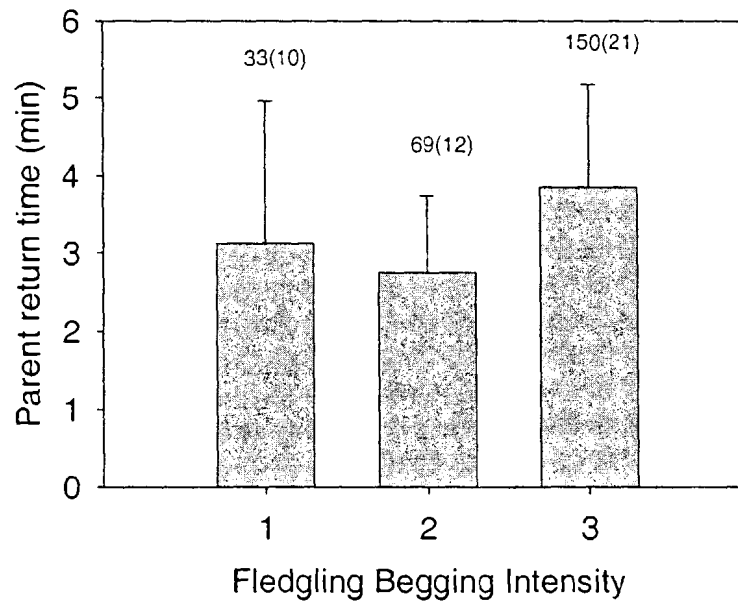
Figure 5 Relationship between the begging intensity of a fledgling and the time taken for a parent to return with the next food item in A) in the first 5 days after nest departure and B) the second week after nest departure. Bars represent LS mean ±95% confidence intervals after controlling for the significant effects of year (in A) and parent sex (in B). The numbers above the bars show the number of observations (number of individuals). In A the data is drawn from 39 individuals from 16 broods. In B the data is drawn from a total of 22 individuals from 11 broods.

hunger but correlated with interannual variation in parental feeding rates suggesting that

begging reflects long-term condition. Parents initially responded to variation in begging

intensity but became less responsive to fledgling begging over the period of dependence,

suggesting there was some conflict over the timing of independence.

Fledgling begging signals: do they reflect short or long-term need?

This study found that the time intervals between feeding events did not influence

begging in fledgling American dippers suggesting that begging intensity does not reflect

short-term hunger. This is in contrast with most studies of nestlings where begging is

positively correlated with short-term hunger (Bengtsson and Ryden 1983, Smith and

Montgomerie 1991). Begging may be more tightly linked to short term hunger in

nestlings because of the higher metabolic costs associated with growth and

thermoregulation. At the fledgling stage, a decreased growth rate and the ability to

supplement provisioning with self-foraging may allow them to stay satiated for longer

periods of time (Marchetti and Price 1989). Alternatively, I may not have detected a

hunger effect if the time lags between feeding events in my study (>20min) were too

short to induce hunger. However, this appears unlikely as studies on nestlings have

frequently detected changes in begging using time lags of a similar magnitude (Redondo

and Castro 1992a, Leonard and Horn 1996, Price et al. 1996, Leonard and Horn 2001a).

Fledgling begging may be more likely to reflect long-term food allocation

patterns in fledglings given the link between fledgling condition and juvenile survival

(Heinsohn 1991, Donnelly and Sullivan 1998). Begging has been shown to reflect long-

term condition in a few studies. Price et al. (1996) showed that nestling yellow-headed

blackbirds in poor condition begged at higher intensities than nestlings in superior

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condition. Interannual variation in begging intensity observed in fledgling dippers results from variation in provisioning rates suggesting that fledgling condition is reduced in the year with lower provisioning rates. The food delivery rate to fledglings was lower (Table 1) and the return times of provisioning parents were longer in 2004 than in 2005 (2004: 5.61min, 2005: 2.85min). Unfortunately, I have no direct measure of fledgling condition during the period I measured delivery rates. However, similar responses to food delivery were found in nestling tree swallows where begging intensity was higher at a site with lower food abundance than at a site with higher food abundance (Hussell 1988). Escalated begging intensities in the year with lower provisioning rates, after controlling for short-term need and sibling competition, suggest that begging in dipper fledglings reflects condition. Further exploration of the impact of food abundance, parental provisioning rates and begging on fledgling condition is needed.

Influence of sibling competition on begging

In many species, social context in the nest influences begging. For example, begging intensifies with increasing brood size (tree swallows: Leonard et al. 2000) and relative competitive ability (American robin (*Turdus migratorius*): Smith and Montgomerie 1991, yellow-headed blackbird: Price and Ydenberg 1995, tree swallow: Leonard and Horn 1998, crimson rosella (*Platycerus elegans*): Krebs 2001). In stark contrast, the begging intensity of fledgling dippers did not increase when spending more time in close proximity to a sibling despite the fact that parents preferentially fed the fledgling begging at the highest intensity. This may in part be due to the fact that the presence of a sibling did not appear to alter the total amount of food an individual obtained. In contrast to my results, great tit (*Parus major*) fledglings that formed dyads

begged at higher intensities and received more food than when they were alone (Sasvári 1990).

Response of adults to begging

In the nest, parents can respond to begging by allocating food in response to variation in begging intensity (Redondo and Castro 1992a, Kilner 1995, Leonard and Horn 1996, Price et al. 1996, Kolliker et al. 1998) or by adjusting their delivery rate (Bengtsson and Ryden 1983, Leonard and Horn 1996, Kilner and Johnstone 1997, Phillips and Croxall 2003). In the nest, parents generally feed the closest, loudest and/or largest nestling (Leonard et al. 1994, Kilner 1995, Smiseth et al. 1998, Smiseth et al. 2003). Experimental studies also suggest that parents frequently use begging cues when making decisions about soon to return with food to the nest (tree swallow: Leonard and Horn 1996, Leonard and Horn 1998, Leonard and Horn 2001b, crimson rosella: Krebs and Magrath 2000, grey-headed albatross (*Thalassarche chrysostoma*): Phillips and Croxall 2003) where inter-trip interval is influenced by nestling signal intensity (Henderson 1975, Bengtsson and Ryden 1983, Hussell 1988, Stamps et al. 1989, Smith and Montgomerie 1991).

Similar parental responses to begging by fledgling dippers were observed early in the post-fledging period. I found that begging intensity of fledgling dippers influenced both allocation decisions and return times of male and female dippers provisioning young fledglings. Similarly, common tern parents allocated care using both fledgling proximity and begging intensity at the approach of a parent (Smith et al. 2005). In great tits, a greater proportion of food was delivered to fledglings begging at the highest intensity (Sasvári 1990).

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Parents and offspring are predicted to frequently be in conflict over the timing of independence (Trivers 1974). In fledglings, this conflict may be expressed as a change in parental responsiveness to offspring solicitation (Davies 1978). Parents can promote independence by decreasing their response to begging or by behaving aggressively towards young (Sullivan 1988, Leonard et al. 1991). Davies found that independence in fledgling spotted flycatchers (*Muscicapa striata*) (Davies 1976) and great tits (Davies 1978) was brought about by both improved juvenile foraging proficiency and reduced provisioning rates by parents. Moreno (1984) showed that, beyond 6 days after fledging, parent northern wheatears (*Oenanthe oenanthe*) no longer brought food to stationary fledglings and only fed fledglings that begged while pursuing them. In my study, parents stopped responding to increases in begging intensity by reducing the time to return with food in the second week. Return times, however, did not increase in the second week, and, if anything, time intervals between deliveries decreased. This is likely because fledglings were more mobile in the second week and often pursued parents on foraging trips until they were fed. I did not quantify load sizes but parents did appear to deliver small items perhaps in an attempt to silence persistent begging. Parents may therefore encourage independence in older fledglings by both reducing provisioning rates and reducing their response to high intensity begging.

Although parents were less responsive to begging in the late post-fledging period there are two reasons that changes in parental behaviour appear unlikely to determine the timing of independence in American dippers. First, many fledglings leave their natal territory within 6-8 days of nest departure when parents are still provisioning at a high rate (see chapter four). Secondly, there was no evidence of parental aggression towards

fledglings at any point in the post-fledging period. The absence of aggression and the departure of young prior to a reduction in feeding rates, suggests there are additional cues determining the timing of independence by the young.

CHAPTER THREE: SEX-DEPENDENT DEVELOPMENT OF FORAGING BEHAVIOUR IN FLEDGLING AMERICAN DIPPERS (*CINCLUS MEXICANUS*).

Introduction

Age-specific differences in foraging behaviour are documented in many species (Marchetti and Price 1989, Wunderle 1991). Juveniles tend to be less proficient at one or more aspects of foraging than adults. Furthermore, adults and juveniles may also differ in their choice of foraging microhabitat (Weathers and Sullivan 1989, Yoerg 1994), choice of prey types (Wunderle 1991, Weathers and Sullivan 1989, Rutz et al. 2006) and type of foraging tactics (Davies and Green 1976, Wunderle and Lodge 1988, Wunderle 1991).

Foraging differences between adults and juveniles may reflect developmental or environmental constraints. Juveniles are smaller than adults and have underdeveloped flight feathers, muscles and motor skills (Marchetti and Price 1989). Additionally, juveniles may have less experience with the capture and handling of prey and consequently have lower foraging efficiency and success than adults (Marchetti and Price 1989, Yoerg 1994). For example, juvenile northern mockingbirds (*Mimus polyglottos*) spent more time foraging, made more attack attempts and achieved lower success rates than adults (Breitwisch et al 1987). Foraging tactics may also differ due to environmental constraints if adults and juveniles forage in different microhabitats (Sutherland et al 1986, Draulans 1987, Marchetti and Price 1989, Edwards 1989). Adult ospreys preferentially foraged in littoral habitats and switched prey types as abundances shifted while juveniles showed no habitat preference and showed consistent prey preferences (Edwards 1989).

To overcome constraints, juveniles may specialize on more accessible but less energetically rich prey types that provide a higher return given their state of development or experience. For example, fledgling white-throated magpie-jays (*Calocitta formosa*) specialized on more easily captured fruits until foraging proficiency on arthropods improved (Langen 1996). Similarly, fledgling Eurasian dippers (*Cinclus cinclus*) specialize on the easily-captured, abundant blackfly (Simuliidae) larvae in the stream margins rather than energetically-rich but less accessible submerged prey (Yoerg 1994). Once juveniles reach breeding age, age-specific differences are still apparent in some species (Langen 1996, Heinsohn 1991) and not in others (Sullivan 1989, Weathers and Sullivan 1989).

Studies that have examined age-specific differences in foraging behaviour and proficiency suggest that skills developed during the post-fledging period impact survival and subsequent behaviour. Lack of foraging proficiency has been shown to impact juvenile survival (Sullivan 1988, Donnelly and Sullivan 1998, Leary et al. 1999) (but see Desrochers 1992). For example, juvenile white-winged choughs (*Corcorax melanorhamphos*) that began to rely on independent foraging by their first winter had higher survival (Heinsohn 1991) than those relying on provisioning from family groups. Foraging proficiency can also influence within-brood variation in timing of independence (Yoerg 1998) and age at first breeding (Ryder 1980, Heinsohn 1991). Variation in foraging skill use and prey specialization in juvenile Eurasian dippers is correlated with timing of independence (Yoerg 1998) while, in white-winged choughs, the ability to care for young is limited by slow development of foraging skills (Heinsohn et al. 1988). Examination of potential factors responsible for variation in the development of foraging

skills is important given the role early foraging behaviour plays in juvenile survival and reproductive success.

This study explores the role of developmental and environmental constraints on the mobility and foraging behaviour of juvenile American dippers (*Cinclus mexicanus*). American dippers are ideally suited to the study of the development of post-fledging behaviour for three reasons. First, adult dippers use a diversity of foraging skills from simpler, energetically inexpensive behaviours to complex, expensive behaviours in terrestrial, aquatic and aerial habitats. Second, American dippers are partial migrants with migrants and residents occupying spatially distinct breeding locations so their fledglings develop in habitats that differ in prey type (Morrissey 2002). Finally, juvenile foraging proficiency influences survival in American dippers (Donnelly and Sullivan 1998) and variation in juvenile foraging tactics appear to influence the timing of independence in Eurasian dippers (Yoerg 1998). Since females typically leave their natal territory before males (Chapter 4), the latter result suggests that females and males may follow different developmental schedules during the post-fledging period. Specifically I, (1) evaluate how developmental factors influence age-related changes in mobility and foraging behaviour of juvenile dippers, (2) compare the behaviour of fledglings produced by migrants and residents to explore the influence of microhabitat differences in prey type on the acquisition of foraging skills and (3) investigate whether sex differences in the timing of departure are associated with sex differences in foraging behaviour during the post-fledging period.

Methods

Study site and study species

I studied American dippers in the Chilliwack River watershed located 150km east of Vancouver, British Columbia, in the Coast Mountain range, from March to July 2003-2005. The watershed consists of 1st to 4th order streams and drains an area of 1,200km^2. American dippers are obligate aquatic passerines that feed on benthic prey submerged in and along the margins of fast-flowing mountain streams (Tyler and Ormerod 1994). Adults use a wide range of foraging techniques including pecking for Simulid larvae and emerged adult insects on rocks and moss, head-dunking to pick prey off rocks and floating in the water column, diving for aquatic invertebrate larvae, salmonid fry and eggs and flycatching for aerial insects (Tyler and Ormerod 1994). Pairs raise broods of 2-5 young and are often double-brooded (Gillis et al. submitted). Dippers have a relatively extended nestling period (mean± SE= 24.9± 0.19 days, range= 19-30 days, N=100) and contracted post-fledgling dependant period (6 days to 3 weeks) compared to other passerines of similar mass (~60g) (Ricklefs 1968, Kingery 1996). Young emerge at full adult mass with well-developed juvenile plumage and are capable of diving and flying short distances upon fledging (Sullivan 1973, Tyler and Ormerod 1994, Kingery 1996).

Nest monitoring and sex determination

Breeding pairs were studied on the main stretch of the Chilliwack River and on 4 of its tributaries. Altitudinal migrant pairs bred more than 3km upstream of the river confluence on tributaries while sedentary resident pairs bred on the main stretch of the river. Pairs were located by visiting territories occupied in previous years and by searching stretches of stream on foot. All pairs were monitored throughout the breeding

season. Each nesting attempt was monitored from nest initiation (nest building) through fledgling independence. Ten to 14 days after hatching each nestling was marked with a unique combination of three darvic colour bands and one US Fish and Wildlife Service aluminum band.

Fledgling sex was determined using a DNA-based test employing PCR amplification of a section the avian CHD1 genes (CHD1-W and CHD1-Z) located on the avian sex chromosomes (see Griffiths et al. 1998, for details of procedure). DNA was isolated from a blood sample ($\sim$0.25μL) taken from the brachial vein of nestlings at the time of banding. The accuracy of the technique was confirmed using blood samples from 18 adults whose sex was determined using behavioural cues during breeding. In all cases, molecular sexing confirmed sexing based on behaviour (N= 5 males, 13 females).

Time budget focal observations

I visited each breeding territory every day from 22 days after hatching to determine exact fledging dates and note the identity of nestlings that fledged. Individuals were located by searching territories on foot, following adults carrying prey and listening for begging calls. Territories were searched by two observers until all brood members were resighted or 2 hours had elapsed. In 2004 and 2005 I attempted to observe all fledglings in each brood 8 times; conducting observations on the first five days after fledging and twice between days 6-8, 9-11 and 12-14. A slightly different protocol was followed in 2003 when only 1 individual per brood was observed at 2 to 3 day intervals from fledging to day 14. On average, individuals were observed 4 times (range: 1 to 8). Sample sizes of each age varied as not all individuals were located on each day and some fledglings had died or left their natal territory before day 14.

Focal fledglings were observed for approximately one hour between 1000h and 1400h on each observation day (mean: 56 min, range: 20-115 min). Individuals were observed using 10X42 binoculars or a 10-60X zoom spotting scope at greater than 10m. The behaviour of the fledgling was recorded every 60 seconds. I distinguished between 4 types of foraging behaviour (pecking, head-dunking, diving and flycatching), 4 types of movement (walking, wading, swimming and flying), preening and standing motionless (see Table 1 for a detailed description of each behaviour). I summed time spent pecking, head-dunking, diving and fly-catching to get the proportion of the total time budget spent foraging and, summed time spent walking, walk-pecking, wading, swimming, diving and flying to get the proportion of time spent mobile. Flycatching was first noted at the end of the second week and was not observed using my sampling protocol so does not contribute to estimates of time spent foraging. In addition, when I first located the fledgling, I recorded the distance from the nest and subsequently kept a record of the distance to the nearest sibling and the cumulative distance travelled throughout the observation period.

Statistical analyses

I used a mixed modelling approach to examine changes in foraging behaviour with time since nest departure of fledgling American dippers since broods contained 2-5 fledglings and individuals were observed between 1 and 8 times. I fitted mixed models to 4 dependent variables (1) the proportion of time spent mobile, (2) the proportion of time mobile spent swimming, diving and flying, (3) the proportion of time foraging (4) the proportion of foraging time spent in the water (ie head-dunking and diving). I examined the influence of 6 explanatory variables; fledgling sex, age at fledging, fledge date, time

since nest departure (1-14 days after nest departure), year (2003-2005) and parental migratory strategy (migrant or resident).

Models were fitted using the 'restricted maximum likelihood' (REML) procedure in Genstat 5.4.1 for Windows (GENSTAT 5 Committee 1997). Initially all models contained all main effects and relevant interactions with individual and brood identified as random terms. However, there was little variance associated with the random term and the standard errors of the variance component were large compared to the mean so the brood term was subsequently dropped (see Legge et al. 2001, for rationale). Final models were selected by systematically eliminating all non-significant interaction terms and then main effects until only significant terms remained. To determine the significance of a variable, the deviance of the full model was compared to the deviance of the submodel containing the same variables, but excluding the variable of interest. The change in deviance approximates a chi-square distribution (Payne 2006). I tested whether models conformed to the assumptions of normality and equal variances by examining residual and normal probability plots.

Results

I monitored an average of 23 pairs per year (2003= 21, 2004= 15, 2005= 24). These pairs produced a total of 150 fledglings. I observed 81 marked fledglings from 23 broods in 2003-2005.

Most nestlings left the nest 25 days after hatching although there was considerable variation in the age at fledging (mean± SE= 24.9± 0.19 days, range= 19-30 days, N=100). Fledglings spent the first day in close proximity to siblings within 10m of the nest.

Fledglings were all capable of flying short distances (up to 3m) diving and swimming to the riverbank if swept away. However, powered flight was initially clumsy and fledglings only began to make longer flights across the river or creek 4 days after fledging.

What factors influenced mobility?

The proportion of the time budget that fledglings were moving did not change significantly with the time since nest departure (time since nest departure: $\chi^2 = 0.4$, df= 1, p= 0.53; Figure 6) although there was a suggestion that females spent less time moving the longer they were out of the nest (time.sex interaction: $\chi^2 = 3.30$, df= 1, p= 0.07). Fledglings spent a greater proportion of their time mobile in 2004 than 2003 and 2005 (LS mean± SE: 2003= 0.32± 0.03, 2004= 0.36± 0.02, 2005= 0.30± 0.02; $\chi^2 = 6.86$, df= 2, p= 0.03). Fledging date and age at fledging, in contrast, had no effect on the proportion of time spent moving (fledging date: $\chi^2 = 0.52$, df= 1, p=0.47; age at fledging: $\chi^2 = 0.02$, df= 1, p= 0.88; fledge date.age at fledging interaction: $\chi^2 = 0.05$, df= 1, p=0.82). Fledglings produced by residents and migrants also spent the same proportion of the time budget moving (LS mean± SE: migrant= 0.34± 0.01, resident= 0.32± 0.03; migratory strategy: $\chi^2 = 0.40$, df= 1, p= 0.53; time.migratory strategy interaction: $\chi^2 = 0.31$, df= 1, p= 0.53).

As they spent more time out of the nest, male fledglings spent a greater proportion of the time that they moved on swimming, diving and flying. Female fledglings, in contrast, did not change the relative contribution of walking, swimming, diving and flying to their time budget (sex.time since fledging interaction: $\chi^2 = 4.03$, df= 1, p= 0.05; Figure 7). Fledglings also spent a greater proportion of their time swimming, diving and flying in 2004 and 2005 than 2003 (LS mean± SE: 2003= 0.11±0.02, 2004= 0.14± 0.02, 2005= 0.14± 0.02; $\chi^2 = 11.16$, df= 2, p= 0.004). Fledging date and age at fledging, in

contrast, had no effect on the contribution swimming, diving and flying made to the time spent on mobility (fledging date: $\chi^2 = 0.13$, df= 1, p= 0.72; age at fledging: $\chi^2 = 2.14$, df= 1, p= 0.14). Fledglings produced by migrants and residents spent a similar amount of their overall time spent moving on swimming, diving and flying (LS mean± SE: migrant= 0.12±0.01, resident= 0.13±0.02; $\chi^2 = 3.25$, df= 1, p= 0.07).

What factors influenced foraging?

Male and female fledglings spent approximately 30% of the time budget foraging independently. Fledglings did not increase the proportion of time spent on foraging the longer they were out of the nest (time since fledging: $\chi^2 = 2.87$, df= 1, p= 0.09; fledgling sex: $\chi^2 = 0.47$, df= 1, p= 0.49; time.sex interaction: $\chi^2 = 0.95$, df= 1, p= 0.33; Figure 8). The proportion of time fledglings spent foraging did not differ among years or in relation to fledging date or age at fledging (year: $\chi^2 = 1.58$, df= 2, p= 0.45; fledge date: $\chi^2 = 0.36$, df= 1, p= 0.55, age at fledging: $\chi^2 = 0.26$, df= 1, p= 0.62; all interactions p>0.1). Fledglings produced by migrants and residents did not differ significantly in the proportion of time spent foraging (LS mean± SE: resident: 0.31±0.48 migrant: 0.19±0.48; $\chi^2 = 0.07$, df= 1, p= 0.80).

Fledglings spent relatively more of their foraging time on head-dunking and diving the longer they were out of the nest. The proportion of foraging time males spent head-dunking and diving increased at a greater rate than females (time since fledging $\chi^2 = 23.52$, df= 1, p= 0.001, sex.time interaction: $\chi^2 = 3.75$, df= 1, p= 0.05; Figure 9). The contribution head-dunking and diving made to the total time spent foraging did not vary with year, fledging date or age at fledging (year: $\chi^2 = 4.54$, df= 2, p= 0.10; fledge date: $\chi^2 = 0.06$, df= 1, p= 0.81, age at fledging: $\chi^2 = 0.03$, df= 1, p= 0.86; all interactions with time

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A
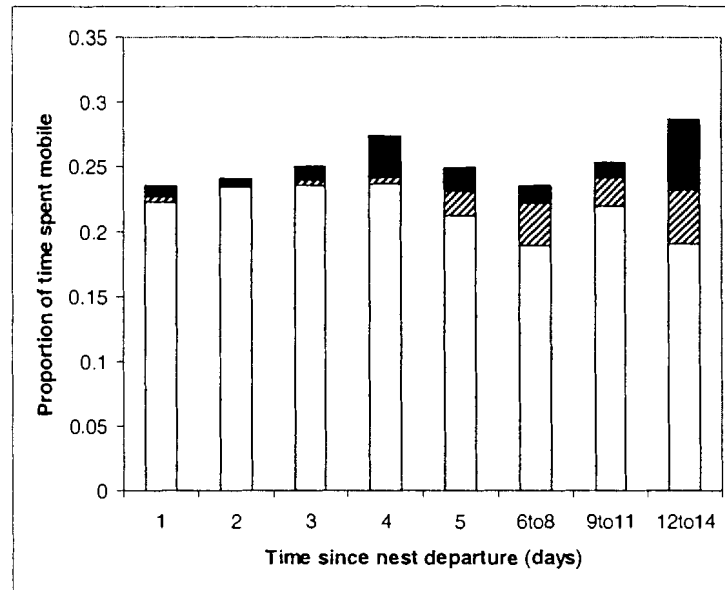
B
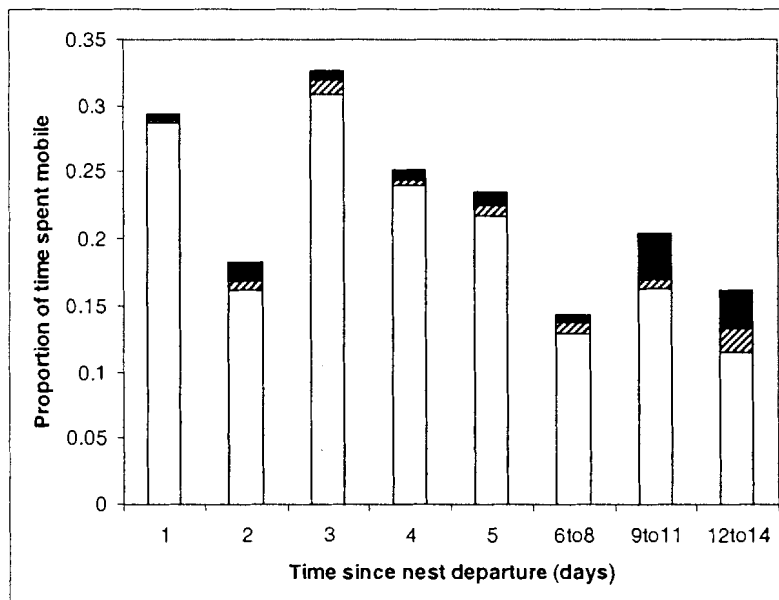
Figure 6 Relationship between the time since nest departure and the proportion of the time budget
(A) male and (B) female fledgling American dippers are mobile. Bars show the
proportion of the time budget spent walking (white bars), diving (hatched bars) and
flying (black bars). Data are drawn from a total of 61 individuals from 20 broods.

35
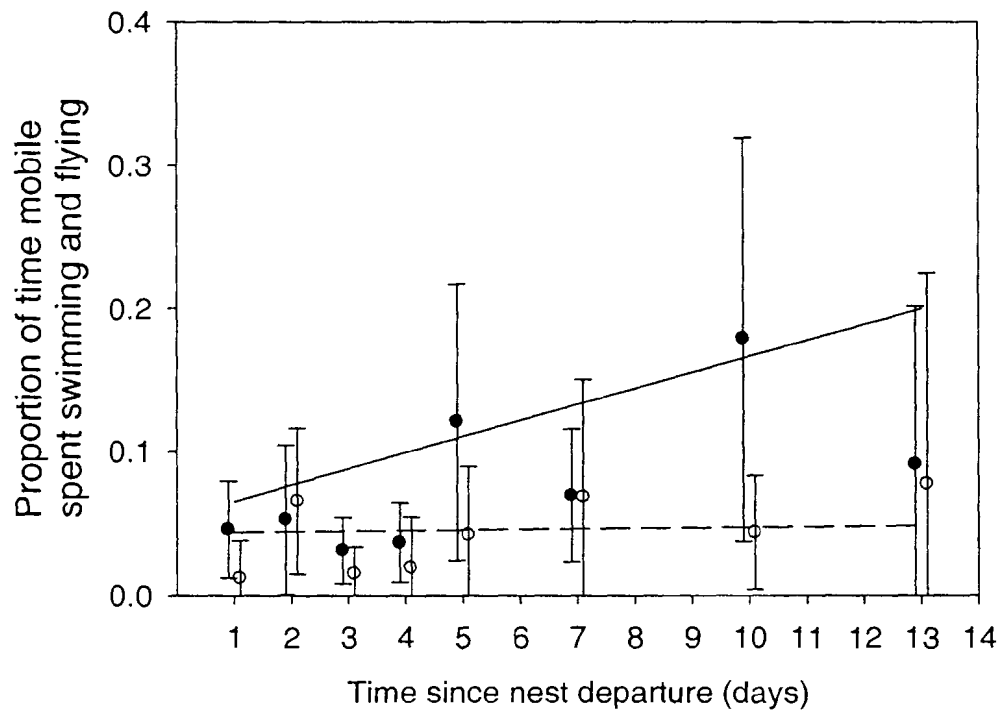
Figure 7 Relationship between the time since nest departure and proportion of the time mobile spent
swimming and flying in fledgling American dippers. Points show mean (± 95% C.I.) for
males (filled circles) and females (open circles) at each time interval. Points are offset
slightly to aid interpretation. Lines show predictions from a mixed model for males
(solid line) and females (dashed line) (sex.time since nest departure: p=0.05), controlling
for the significant factors migratory strategy and year. Data are drawn from a total of
38 males and 23 females from 20 broods.

A
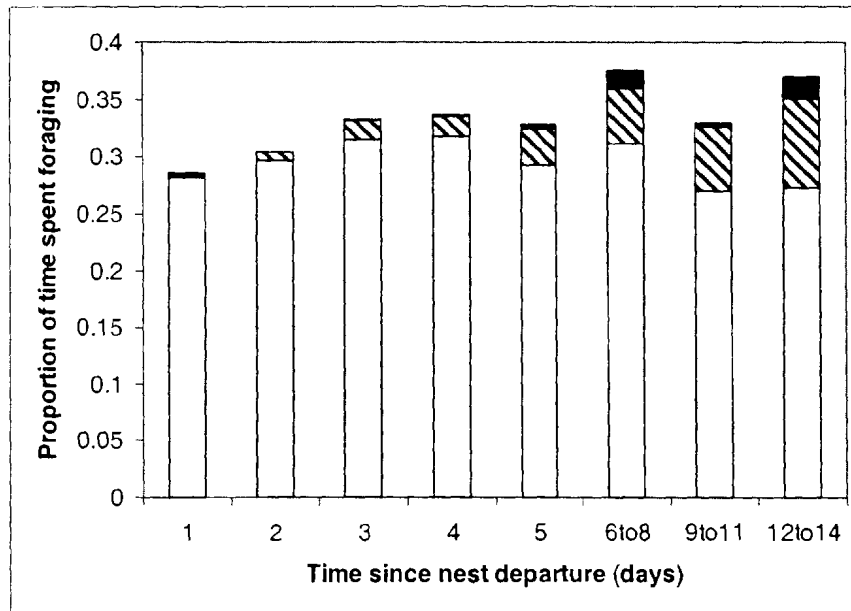
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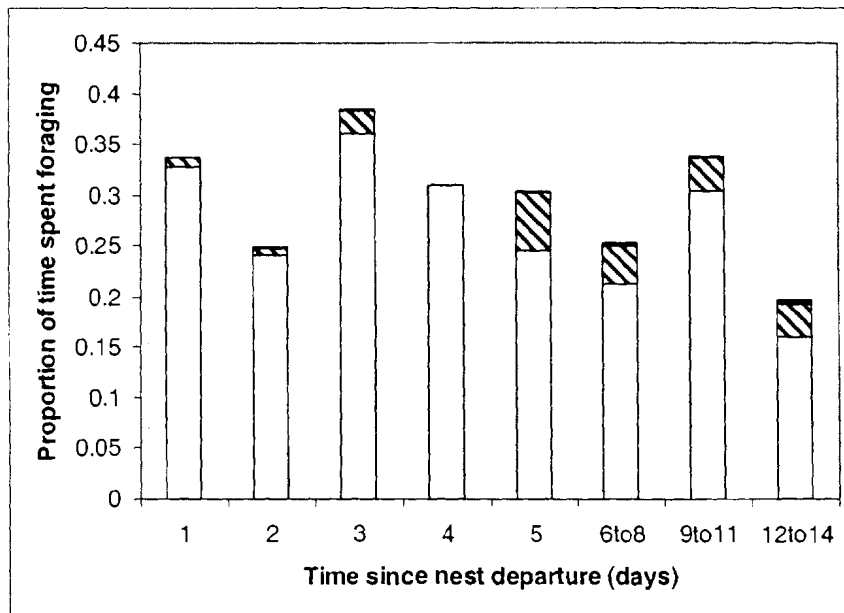
Figure 8 Relationship between the time since nest departure and the proportion of the time budget
spent foraging by (A) male and (B) female fledgling American dippers. Bars show the
proportion of the time budget spent pecking (white bars), head-dunking (hatched bars)
and diving (black bars). Data are drawn from a total of 61 individuals from 20 broods.
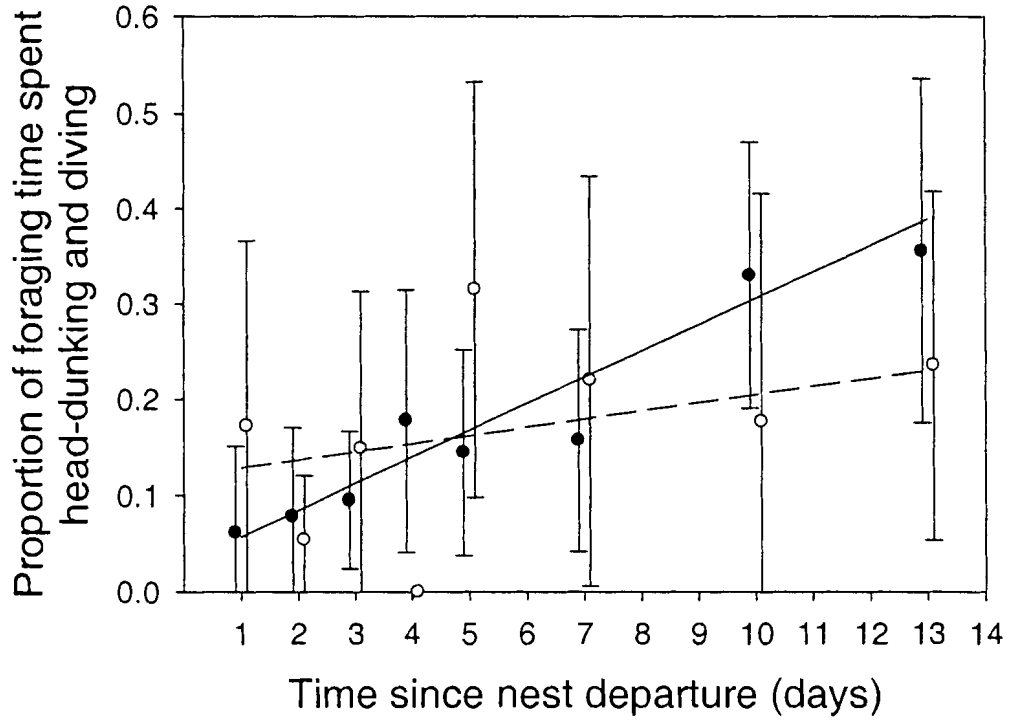
Figure 9 Relationship between time since nest departure and proportion of time foraging spent head-dunking and diving by fledgling American dippers. Points show mean (± 95% C. I.) for males (filled circles) and females (open circles) for each time interval. Points are offset slightly to aid interpretation. Lines show prediction from a mixed model for males (solid lines) and for females (dashed lines) (sex.time since nest departure: p=0.05). Data are drawn from a total of 38 males and 23 females from 20 broods.

p>0.1). Fledglings produced by residents and migrants spent the same proportion of foraging time on head-dunking and diving (LS mean± SE: resident: 0.16±0.05, migrant: 0.14±0.05; χ^2= 0.21, df= 1, p= 0.65).

Discussion

Age-specific foraging differences observed in birds are often attributed to developmental or environmental constraints on juveniles (Marchetti and Price 1989). Juvenile size or plumage development can constrain foraging behaviour if small young are not capable of performing physically challenging behaviours. Behaviours requiring greater muscular strength or well-developed motor control may, therefore, only be represented in the behavioural repertoire of older individuals (Davies 1976, Davies and Green 1976). For example, fledgling northern wheatears (*Oenanthe oenanthe*) began to use the more challenging 'perch-to-ground-sallying' and 'aerial-hawking' after being out of the nest for 5 days (Moreno 1984). My data and previous work on dippers provides some support for this hypothesis. Juveniles spent more of their total foraging time on foraging behaviours that might be expected to require greater strength or motor control (Bryant and Tatner 1988) the longer they were out of the nest. Head-dunking to capture prey floating in the water column or attached to rocks, and diving in fast-flowing water were not observed immediately following nest departure and flycatching began to occur only at the end of the second week after nest departure (this study, Donnelly and Sullivan 1998, Yoerg 1994, 1998). However, two results suggest that increased size and motor control are unlikely to be the most important factor explaining changes in mobility and foraging behaviour in fledgling American dippers. Firstly, age at fledging, despite ranging from 19 to 30 days after hatching, did not influence the amount of time spent on

foraging or the foraging tactics used by fledgling dippers. Secondly, unlike most passerines, American dippers have an extended nestling period and fledge at 95% of adult mass. Flight feathers may continue to grow after fledging gradually reducing the energetic costs of swimming and flying. However, since adult males and females are not known to use different foraging tactics, post-fledging flight feather growth is unlikely to explain the observed sex differences in fledgling mobility and foraging behaviour.

Improvement in foraging behaviour over time may also occur because juveniles require experience at capturing and handling prey before becoming proficient. Improvement in foraging behaviour may occur as young gain experience at foraging on prey encountered on the natal territory. For example, variation in foraging tactics between individual Eurasian dippers was attributed to specialization on prey successfully subdued during early foraging attempts (Yoerg 1994). We found no evidence that fledgling foraging behaviour differed between years that varied in parental provisioning rates (see chapter two) or between migrant and resident territories known to differ in prey type (Morrissey 2002). While experience with capturing and handling prey may explain the increase in the use of aquatic behaviours over time, experience does not account for the observed sex-specific differences in development of foraging behaviour.

Variation in habitat structure has been shown to produce differences in foraging behaviour between individuals. Adult and juvenile ospreys foraged on different prey and in different habitats during the post-fledging period producing differences in skill use between the age classes (Edwards 1989). Migratory and resident dippers breed in territories that differ markedly in habitat structure. Higher elevation migratory territories are characterized by steep stream margins and turbulent water while lower elevation

resident territories have lower-lying banks and less altitudinal relief (Morrissey 2004). Fledglings produced by migrants were more likely to spend a greater proportion of the time they spent moving on swimming and flying than fledglings produced by residents. Differences in habitat structure between migrant and resident territories may result in differences in mobility between young born to migrants and residents. Migrant-born young may be forced to spend more time flying to navigate around steep banks and large boulders. However, any differences in habitat structure associated with breeding on the river or a creek had no affect on the amount of time spent foraging or the foraging behaviours used suggesting that environmental factors did not play a major role in the development of foraging behaviour.

Both developmental and environmental factors failed to explain the sex differences in mobility and foraging behaviours observed during the post-fledging period in this study. An alternative explanation for this pattern is that sex-differences in timing of natal dispersal select for different developmental schedules in juvenile males and females. In American dippers, females leave their natal territory sooner after nest departure than males and therefore may need to be energetically self-sufficient before males. Yoerg (1998) argued that early dispersal in juvenile Eurasian dippers may select for individuals that specialize on easily captured, less energetically rich prey. She found that juveniles that specialized on easily-captured prey departed at younger ages than those that use the full repertoire of foraging behaviours. She did not have information on the sex of the fledglings so was unable to address the potential for sex differences in the development of foraging behaviour. My study suggests that, prior to dispersing, females are using simpler foraging tactics to specialize on easily-captured prey while males use a

greater diversity of foraging behaviours. Whether dispersal strategies select for sex-specific developmental schedules would require examination of whether sex-specific foraging behaviours are maintained into the first winter. This investigation is warranted given the importance of foraging behaviour on juvenile survival in dippers (Donnelly and Sullivan 1998).

CHAPTER FOUR: CAUSES OF VARIATION IN TIMING OF DEPARTURE IN FLEDGLING AMERICAN DIPPERS (*CINCLUS MEXICANUS*).

Introduction

Natal dispersal impacts gene flow (Greenwood 1980, Dieckmann et al. 1999), demographic stability (Greenwood 1980, Martin et al. 2000) and the potential for evolutionary change (Johnson and Gaines 1990) and is therefore a critical process in avian life history. Natal dispersal is initiated when individuals leave their natal territory to search for a wintering or breeding vacancy. The timing of natal departure is known to have consequences for subsequent survival (Ekman and Rosander 1992, Ekman et al. 1999) and lifetime reproductive success (Ekman et al. 1999, Ekman et al. 2002). Studies have therefore begun to focus on the causes and consequences of variation in the timing of natal departure.

Timing of natal departure in birds shows wide variation both among and between species. In general, juveniles begin to leave their natal territory within a few weeks of nest departure (nuthatch (*Sitta europaea*) 2-4wk: Currie and Matthysen 1998; wood thrush (*Hylocichla mustelina*) 3wks: Anders et al. 1998, Vega Rivera et al. 1998; eastern meadowlark (*Sturnella magna*) 3wk: Kershner et al. 2004; carrion crow (*Corvus corone*) 5wk: Baglione et al. 2006; northern goshawk (*Accipiter gentilis*) 4-9wks: Wiens et al. 2006). In contrast, juveniles in cooperatively- breeding species may defer dispersal for many months (Stacey and Koenig 1990). Within species there is also considerable variation in the age at which juveniles leave their natal territory. For example, in the

socially-monogamous brown thornbill (*Acanthiza pusilla*), some individuals may leave after 6 weeks while others delay departure until the onset of the following breeding season (Green and Cockburn 2001). Similarly, in the cooperatively-breeding superb fairy-wren (*Malurus cyaneus*), females either leave 1-14 weeks or 7-10 months after fledging while males may remain on their natal territory for their entire lifetime (Mulder 1995).

Variation in timing of natal departure in socially monogamous species has been attributed to general intrinsic, environmental and behavioural factors. General intrinsic factors are fixed traits internal to the individual and are frequently genetically determined, while environmental factors are external and are a result of variation in the physical environment. Gender and level of dominance may be considered intrinsic traits of an individual that influence departure (Dhondt 1979, Strickland 1991). Females generally depart their natal territory in advance of males (Dhondt 1979, Strickland 1991). Dominance can promote delayed departure by forcing early departure of subordinate siblings or excluding subordinates from access to resources (Nilsson and Smith 1988). Environmental factors such as conditions on the natal territory (Nilsson and Smith 1985) and natal habitat quality (Newton and Marquiss 1983) can influence departure. Juveniles typically depart sooner from poor quality territories and remain longer on higher quality territories. Recent studies have explored how the behavioural phenotype of an individual influences dispersal decisions. Dingemanse et al. (2003) found that an individual's behavioural response to exposure to a novel object or environment and an individual's exploratory tendency are positively correlated with dispersal distance. These behavioural phenotypes are internal to the individual and may have a genetic component but their

expression is influenced by the abiotic and social environment (Dingemanse et al. 2003, Dingemanse and de Goede 2004).

The choice of when to depart the natal territory is known to impact the distance travelled to find a vacant territory (Nilsson 1989, Green and Cockburn 2001), survival (Ekman and Rosander 1992, Ekman et al. 1999) and lifetime reproductive success (Ekman et al. 1999). In some species, early departure may assure dominant status in a winter flock (Ekman and Askenmo 1984, Eden 1987, Nilsson and Smith 1988) and/or promote access to a nearby, high-quality territory (Drent 1984, Lens and Dhondt 1994). In other species, young that delay departure benefit from access to local food sources that enhance survival (Ekman and Rosander 1992, Ekman et al. 1999), while also increasing the likelihood they obtain a local breeding vacancy (Ekman et al. 1999, Green and Cockburn 2001, Ekman et al. 2002).

Since departure decisions can have long-term consequences, it is important to understand the causes of variation in timing of departure. This study explores the causes of variation in the timing of natal territory departure in American dippers (*Cinclus mexicanus*). Dippers are a model system to examine the causes and consequences in timing of natal territory departure because fledglings are easily located, timing of natal dispersal is known to vary in Eurasian dippers (Yoerg 1998), and adults and juveniles aggregate on accessible, lower elevation streams in winter allowing juvenile survival to be evaluated Specifically, this study will (1) investigate variation in timing of departure, (2) examine how general intrinsic, behavioural and environmental factors influence departure decisions and (3) determine the effects of departure decisions on local survival to recruitment age of males.

Methods

Study area and study species

I studied the American dipper population within the Chilliwack River watershed (49°0'N, 121°4'W). The Chilliwack River is located approximately 100km east of Vancouver in the Coast Mountain Range of southwestern British Columbia, Canada. It is 43.5km in length, fed from the east by Chilliwack Lake and drains an area of 1,200km^2. My study was conducted at eight locations (totalling 16km) on the main stretch of the river and locations on five tributaries (totalling 10km). This population is composed of both migratory and sedentary individuals (residents). Migrants make seasonal movements between breeding areas on higher altitude tributaries and wintering areas on the main stretch of the river (nest altitudes: 28-800m). Resident individuals retain year round multi-purpose territories on the main stretch of the river (Morrissey 2004).

American dipper pairs raise broods of 4-5 young, are occasionally double-brooded with an extended nestling period (24-26 days) and a comparatively short post-fledging dependant period (6 days to 2 weeks) (Kingery 1996, chapter 2). Adults provision young until they depart their natal site (Kingery 1996, chapter 2).

Monitoring of breeding and territory departure

From 2003-2005, 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 USFWS band. Nestlings were weighed and measured at the time of banding. Mass was measured to 0.25g using a Pesola spring balance, tarsus to 0.5mm using calipers and wing to 1mm using a wing

ruler. Daily visits were made to breeding territories when nestlings were 22 days old until the brood fledged in order to determine 1) exact fledging dates and 2) the total number of fledged young. The fledge date (day 1) was the day when the majority of the brood left the nest. I subsequently monitored fledglings by visiting territories on days 1-5 after nest departure, and then every 2-3 days until all young had disappeared or 14 days had elapsed. Fledglings were relocated 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 hours had elapsed. It was not possible to relocate all brood members on all days, however surviving missed young were often relocated on subsequent days. Individual departure date was determined by the midpoint between the last resighting and the subsequent territory visit.

Nestling sex determination, condition and individual behavioural traits

Fledgling sex was determined using a DNA-based test employing PCR amplification of a section the avian CHD1 genes (CHD1-W and CHD1-Z) located on the avian sex chromosomes (see Griffiths et al. 1998 for details of procedure). DNA was isolated from a blood sample (~0.25µL) taken from the brachial vein of nestlings. Condition at banding was estimated using the residuals from a logistic growth curve fitted to nestling mass. Curves were fitted separately for males and females as American dippers are sexually dimorphic and male nestlings were larger than females at 18 days after hatching.

Focal observations were used to determine time budgets of all fledglings found on their natal territory in the first 5 days after fledging. Focal observations lasted approximately one hour on each observation day (mean: 57 min, range: 30-65 min). I

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used mixed models to examine changes in 1) the proportion of time individuals were mobile, 2) the proportion of time mobile they were swimming, diving and flying, 3) the proportion of time spent foraging independently and 4) the proportion of foraging time spent in the water (see chapter three for further details) with time since nest departure. For each model examining age-related changes in behaviour, I generated a Best Linear Unbiased Predictor (BLUP) for each individual. BLUP scores quantify the repeatability of an individual's behavioural patterns and represent the individual's tendency relative to the population mean score (Piepho 2006).

Determination of survival

Residents and migrants aggregate on the Chilliwack River during the winter (Morrissey 2004) permitting resightings of marked individuals. Population censuses were conducted along 16 km of river habitat in the first week of November, January, March, May and July from 2003-2006. Two observers searched 8 river sites on foot using binoculars (8X42) and a spotting scope (20-60X zoom) (see Morrissey 2004 for details). Censuses allowed us to resight fledglings and thus estimate juvenile survival. Juveniles were considered to have survived to recruitment age if they were resighted in March or later in the year following birth. Fourteen percent (44/318) of fledged young in this population are resighted at recruitment age or later (census data 1999-2006, C. A. Morrissey and D. J. Green, unpublished data).

Statistical analyses

I used a Kaplan-Meyer time-to-event analysis to examine when an individual left the natal territory (ie had died or dispersed). The age that fledglings died or dispersed was

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estimated as the mean age between their age when last final resighted and their age on the subsequent territory visit. Individuals were censored if they were still present on the natal territory on the final visit to the territory.

I initially explored departure decisions using a mixed modelling approach since broods consisted of 2-5 individuals. I examined how 4 general intrinsic, 3 environmental and 4 behavioural factors influenced 1) whether an individual was still present or had disappeared at 14 days and 2) variation in timing of departure for those individuals that left the natal territory between 6-14 days after nest departure. General intrinsic factors considered included fledgling sex, fledge date, age at fledging and condition as a nestling. Environmental factors included parental strategy (migratory or resident) and year. Behavioural factors included: 1) time spent mobile, 2) time spent foraging independently, 3) proportion of mobile time spent swimming and diving and 4) proportion of independent foraging time spent submerging the head and diving. All models initially used brood identity as a random term. However, there was little variance associated with the random term and the standard errors of the variance component were large compared to the mean so the brood term was subsequently dropped simplifying the analyses (see Legge et al. 2001 for rationale). Initial mixed models and subsequent generalized linear models were then fitted using Genstat 5.4.1 for Windows (GENSTAT 5 Committee 1997). A similar modelling approach was used to investigate what factors influenced 1) survival to 6 days after nest departure and 2) survival to recruitment age for juvenile males. In all 4 models I initially fitted a full model and all relevant interaction terms. Final models were selected by systematically eliminating all non-significant interaction terms and then main effects until only significant terms remained. Significance of terms

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was assessed using the change in deviance when the term of interest was dropped from the model. I tested whether models conformed to the assumptions of normality and equal variances by examining residual and normal probability plots.

Results

I monitored an average of 23 pairs per year (2003= 29, 2004= 15, 2005= 24). These pairs fledged up to two broods each year containing 2-5 young per brood. Nestlings left the nest approximately 25 days after hatching (mean± SE= 24.9±0.19 days, range= 19-30 days, N=100). A total of 150 fledglings were produced over the course of this study. I monitored the timing of departure of 100 marked individuals (60 males and 40 females) from 30 broods.

General departure pattern

Twenty-two fledglings (N=100) disappeared from their natal territory in the first 5 days after fledging. These individuals were assumed to have died since individuals disappearing in this period were never resighted in winter or spring censuses of the population (0 of 100 fledglings 2003-2006). Of the 78 young surviving to 5 days after nest departure, timing of territory departure was known for sixty-four of these individuals. These young were assumed to have dispersed as young leaving 6 days or more after nest departure were observed outside their natal territory at a later date. A further 29 left between 6-12 days after nest departure. Thirty-five fledglings were still on their natal territory during the last census 12-14 days after nest departure (35/64) (Figure 1). The Kaplan-Meyer model estimates that 12-14 days after fledging 55% of males and 65% of females had either died or dispersed (Figure 10).

Causes of variation in timing of departure

Two of the four general intrinsic factors influenced whether individuals that survived to day 5 remained on their natal territory for longer than 12-14 days. Males were more likely to be present on the natal territory 12-14 days after nest departure than females (χ^2= 9.28, df= 1, p= 0.002). Young that fledged later in the season were also more likely to be present on the natal territory 12-14 days after nest departure than young born earlier (χ^2= 16.67, df= 1, p= 0.001, Figure 11). Condition, measured during the nestling period (χ^2= 2.32, df= 1, p= 0.13), and age at fledging (χ^2= 0.85, df= 1, p= 0.36) did not influence the likelihood of remaining on the natal territory beyond 12-14 days. None of the environmental factors considered influenced whether an individual remained on their natal territory 12-14 days after nest departure (year: χ^2= 0.22, df= 2, p= 0.9; strategy: χ^2= 0.88, df= 1, p= 0.35). No measure of an individual's tendency to move or forage independently influenced whether they were present at 12-14 days (all p>0.1).

The same factors explained variation in the timing of natal departure of young that survived to 6 days and dispersed within 12-14 days of fledging. Females remained on their natal territory for less time than males (χ^2= 2.19, df= 1, p= 0.03). In addition, individuals that fledged earlier in the season spent less time on their natal territory before departing than individuals that fledged later (χ^2= 2.90, df= 1, p= 0.005). Condition as a nestling (χ^2= 1.33, df= 1, p= 0.23) and age at fledging (χ^2= 0.8, df= 1, p= 0.58) did not influence variation in timing of departure. Year (χ^2= 0.46, df= 2, p= 0.64) did not influence variation in departure. No measure of an individual's tendency to move or forage independently influenced how much time they spent on the natal territory before departing (all p>0.1).

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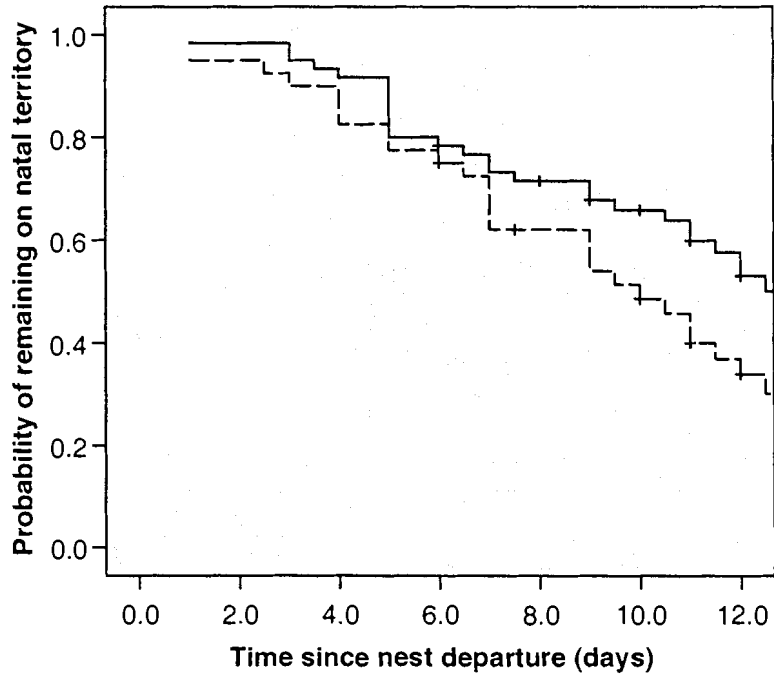
Figure 10 Time-to-event analysis showing the time 60 male (solid line) and 40 female (dotted line) juvenile American dippers were last observed on their natal territory (N=100 individuals from 30 broods (2003-2005). Crosses indicate censored data points.
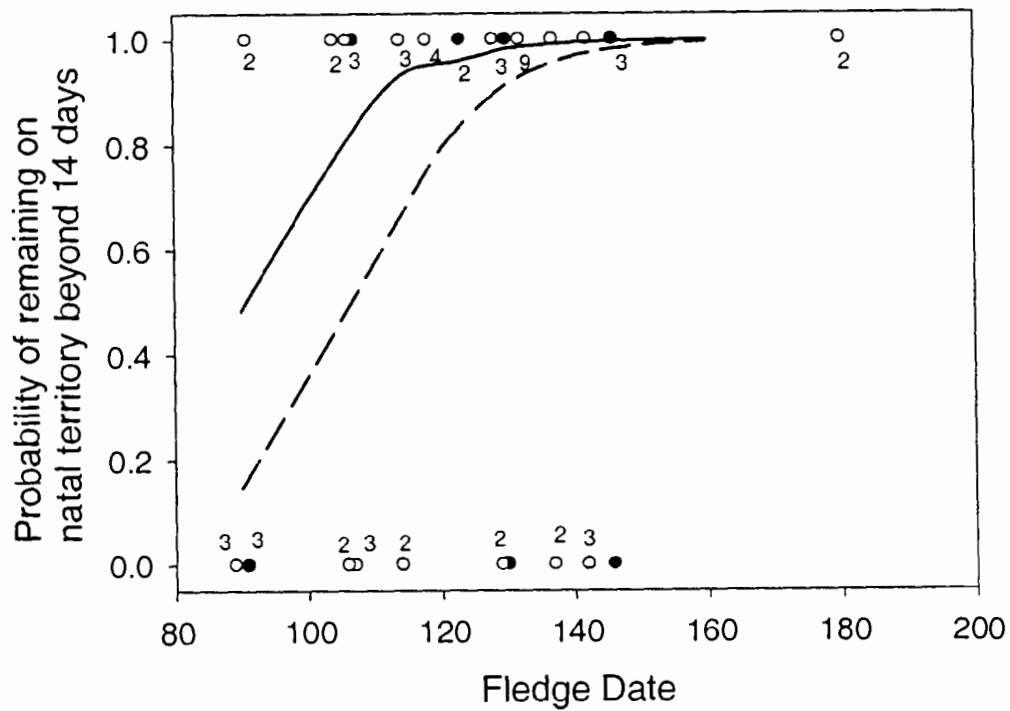
Figure 11 Relationship between fledging date and probability male (filled circles) and female (open circles) fledgling American dippers will be present on their natal territory at 12-14 days after nest departure. Lines show prediction from a mixed model for males (solid lines) and for females (dashed lines). Data are drawn from a total of 64 individuals from 18 broods.

Local survival and recruitment patterns

Male and female fledglings were equally likely to survive to six days after nest departure (predicted value± SE: males: 0.92± 0.04, females: 0.86± 0.06; χ^2= 0.99, df= 1, p= 0.32). However, young that fledged early in the season tended to be more likely to survive to 6 days after nest departure than those that fledged later (χ^2=3.28, df=1, p=0.07). Condition as a nestling (χ^2= 0.19, df= 1, p= 0.67) and age at fledging (χ^2= 0.04, df= 1, p= 0.85) showed no impact on survival to 6 days. Migratory strategy (χ^2= 0.36, df= 1, p= 0.55) and year (χ^2= 0.53, df= 2, p= 0.77) also did not influence survival to 6 days.

Males were more likely to be resighted at an age when they could recruit to the breeding population (males: 6/47 that survived to 6 days, females: 1/30 that survived to 6 days; Fisher's exact test p= 0.13). I therefore only examined how departure decisions influenced survival to recruitment age for males. Males present on the natal territory 12-14 days after nest departure were more likely to be resighted at recruitment age than males departing 6-12 days after nest departure (χ^2=3.88, df=1, p=0.05) (Figure 12). Fledge date (χ^2= 1.78, df= 1, p= 0.18), age at fledging (χ^2= 0.79, df= 1, p= 0.37) and condition as a nestling (χ^2= 1.21, df= 1, p= 0.27) did not influence probability of surviving to recruitment age for males. Migratory strategy (χ^2= 0.001, df= 1, p= 0.95) did not influence survival to recruitment age. No behavioural tendencies influenced survival to recruitment age for males (all p>0.1).
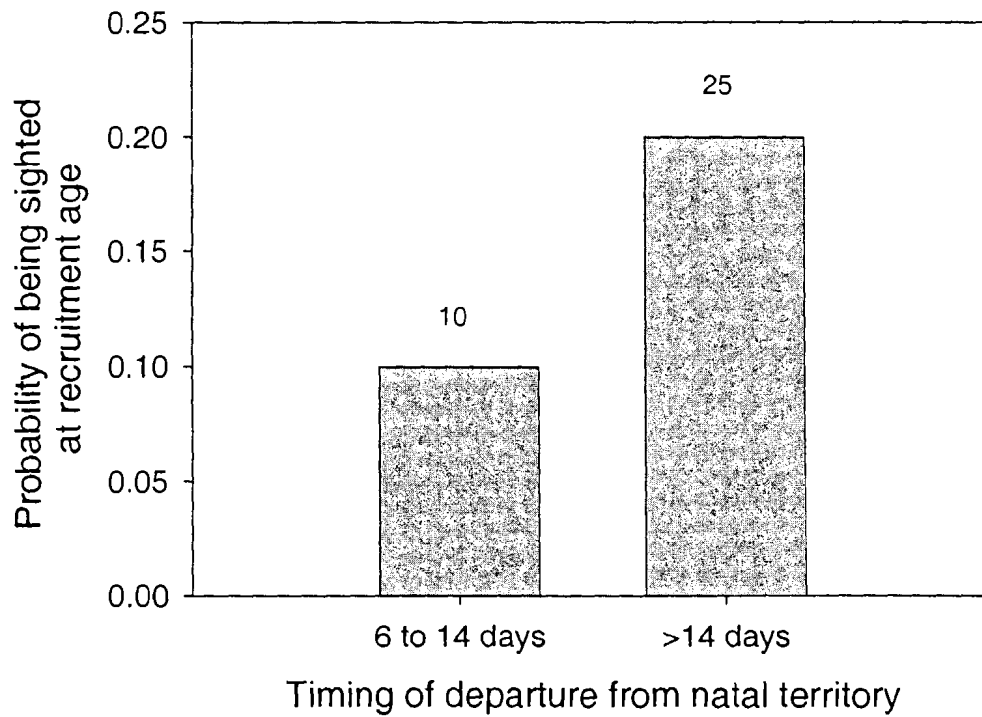
Figure 12 Relationship between timing of departure from the natal territory and subsequent resighting probability at recruitment age in male juvenile American dippers (*Cinclus mexicanus*). Bars represent model estimates from a mixed model. Numbers above bars indicate number of individuals. Data is drawn from a total of 53 individual fledglings from 27 broods (2003-2005).

Discussion

Recent studies suggest that intrinsic, environmental and behavioural factors may all play a role in producing intra-specific variation in avian dispersal strategies. Typically, studies examining whether intrinsic factors influence the timing of natal dispersal have found that females spend less time on their natal territory before dispersing than males (Dhondt 1979, Strickland 1991, Walters et al. 1992). Some studies have also demonstrated that individuals that fledge early in the season spend less time on their natal territory than individuals that fledge late in the season (Mulder 1995, Cockburn et al. 2003). Studies examining how environmental factors influence the timing of dispersal show that young from poor quality territories disperse earlier than young from high quality territories (Nilsson and Smith 1985, Newton and Marquiss 1983, Dufty and Belthoff 2001). No studies to date have examined how the behavioural phenotypes of individuals influence the timing of dispersal or simultaneously examined the relative importance of intrinsic, environmental and behavioural factors in explaining variation in how long fledglings spend on their natal territory before dispersing. I found that two general intrinsic factors influenced the timing of natal departure in American dippers; females departed sooner than males and young from early-season broods spent less time on their natal territory than those from later broods. This study therefore suggests that general intrinsic factors are more important than environmental or behavioural factors in explaining variation in the timing of natal dispersal in this species.

What influences post-fledging survival to dispersal age?

Seasonal variation in juvenile survival is one of the most common patterns documented in birds. In many species, young from earlier broods have higher survival than young born later (Lack 1966, Perrins 1970, Hatchwell 1991, Spear and Nur 1994). This pattern is often attributed to older, experienced adults initiating breeding attempts early in the season. In dippers, survival to six days after nest departure was influenced by fledging date. Young fledging earlier in the season were more likely to survive to six days after nest departure than young fledging later. Previously banded and presumably older birds initiated breeding earlier in the season than unbanded birds that moved into the study area (H. Middleton, C. Morrissey unpub. data) suggesting that older, more experienced birds are higher-quality individuals. Adult age or experience may have influenced the survival of fledgling dippers. In several species, post-fledging survival is influenced by condition as a nestling, which is attributed to parental quality. We cannot demonstrate a direct effect of condition on early survival patterns as there is no evidence that nestling condition is higher earlier in the season. It is unclear whether higher fledgling survival earlier in the season can be attributed to parental experience or the superior quality of territories held by older, experienced breeders.

What factors influence when juveniles leave their natal territory?

Timing of departure from the natal territory varies in many species (eg. Koenig et al. 1992, Currie and Matthysen 1998, Kershner et al. 2004, Baglione et al. 2006, Wiens et al. 2006). In this study, male fledglings were twice as likely as females to be present on their natal territory 12-14 days after nest departure. This pattern has been described in several other species of socially-monogamous birds (Green and Cockburn 2001, Dhondt

1979, Strickland 1991). For example, in brown thornbills, females dispersed in the first three months after fledging while males either dispersed at the same time as females or delayed dispersal for up to 6 months (Green and Cockburn 2001). This pattern is even more striking in many cooperative-breeding species where females typically disperse soon after reaching independence while males delay departure and remain on their natal territory for extended periods (Brown 1987).

Reports of seasonal effects on variation in timing of departure are rare but there are several proximate reasons that may explain why early-season young depart their natal territory soon after fledging. Firstly, young from early broods may be forced to leave their natal territory by parents that terminate care to initiate a second brood. Departure may be promoted by parental aggression towards fledglings (Sullivan 1988, Leonard et al. 1991) or reluctance to provide extended care to young from first broods (Kluijver 1951, Verhulst and Hut 1996). This explanation appears unlikely to explain seasonal changes in the likelihood that juvenile dippers remain on their natal territory for more than 12-14 days as, after controlling for sex, fledglings originating from broods where parents renested were as likely to delay dispersal as fledglings from broods where parents did not renest (renest: 0.78± 0.06, don't renest: 0.66± 0.30; GLM: X^2: 0.75, df= 2, p= 0.69). Alternatively, if early-season young spend more time in the nest or have higher growth rates as a nestling they may fledge in better condition than late-season young and consequently be able to leave their natal territory sooner. In many species, young born earlier in the breeding season are in better condition than young born later (Lack 1966, Perrins 1970, Hatchwell 1991, Spear and Nur 1994). However, in our study, the length of the nestling period did not vary with fledging date (one-way ANOVA: F_1=0.03, p=0.87)

and the age at fledging did not influence the timing of departure ($\chi^2 = 0.07$, df= 1, NS) suggesting that the level of maturity at fledging did not impact early departure of dippers from early-season broods. Finally, if individuals from early-season broods are larger than individuals from later-season broods, they may be able to achieve departure size at an earlier age and spend less time on the natal territory. I found some support for this hypothesis as I detected seasonal variation in age-specific size (one-way ANOVA: $F_1 = 4.65$, p=0.03) with young born early being larger for their age than young born later. Larger age-specific size in early-season young could permit early departure of early-season young. These individuals have either grown at a greater rate or fledge at close to adult size compared to later season young allowing them to depart their natal territory at a younger age. Therefore, the larger size of early-season young gives them the ability to depart at a younger age.

Ultimately, early-season young may spend less time on their natal territory compared to late-season young because the benefits of early departure for these young select for a short post-fledging period. In marsh tits (*Parus palustris*), young that disperse sooner are the first to join winter flocks, have a higher dominance rank and are therefore more likely to fill a breeding vacancy (Nilsson and Smith 1985, 1988). In American dippers, early-season young could potentially benefit by acquiring a high-quality moulting site, arriving early in a wintering area or having more time to prospect for suitable territories. Late summer moult in dippers involves synchronous loss of most primary feathers (Pyle and Howell 1997) resulting in a period of flightlessness (Tyler and Ormerod 1994). Individuals departing at a young age may be competing for good-quality moulting habitat making departure at a young age potentially advantageous. In addition,

juvenile dippers are less philopatric than adults that begin to defend wintering territories in the fall (I. Whitehorne, unpub. data) suggesting that juvenile movements during late summer and fall may be used to obtain information about potential wintering or breeding sites. Although feasible, we have little data at this time to suggest early dispersal leads to fitness benefits. The limited number of females resighted, however indicates that females, and possibly early dispersers in general, may be moving further than the bounds of our study area.

Recent studies have documented interesting relationships between the behavioural phenotypes of juveniles, notably their response to novel objects (neophobia) and exploratory behaviour, and their subsequent dispersal behaviour (Dingemanse et al. 2003). Dingemanse et al. (2002, 2003) found that exploratory behaviour in Great tits is both heritable and predicts natal dispersal distance. In this study, I found no relationship between the timing of natal departure and tendencies to move, forage independently or use aquatic and aerial skills while mobile or foraging. There are two reasons why this might be the case. Firstly, although these behaviours are potentially related to the ability of juveniles to move through the environment and forage independently they are more general than the behaviours examined in previous studies. Secondly, the behaviour of individuals was sampled at a relatively early age. Previous studies of exploratory behaviour performed measurements on recently independent juveniles entering the dispersal stage where behavioural patterns reflect decisions currently being made. Future studies on the relationship between behavioural phenotypes and dispersal decisions may need to focus on species-relevant exploratory behaviours during the age at transition to

independence at which point variation in behavioural tendencies may be more transparent and relevant to dispersal decisions.

Survival to departure and recruitment age

Recent studies suggest that males of both socially-monogamous and cooperative birds may benefit from delayed dispersal. In the socially-monogamous brown thornbill, males that delayed dispersal were more likely to inherit their father's territory, move to a nearby vacant territory or acquire a small portion of their natal territory (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). Young jays that stayed behind also benefited from access to food stores on the natal territory (Ekman et al. 2002). In the cooperative-breeding long-tailed tit (*Aegithalos caudatus*), individuals that delay dispersal to help raise siblings have increased lifetime reproductive success (MacColl and Hatchwell 2004). My study showed a survival advantage to males that delayed departure. Delaying males were more likely to be resighted at recruitment age suggesting they benefited from increased survival and likelihood of acquiring a local breeding vacancy. Of the 25 males that were known to delay departure, 5 survived to recruitment and 4 filled breeding vacancies between 1-5km from their natal territory. In contrast to males, females were less likely to remain on the natal territory and appear to obtain less benefit from delayed dispersal. Female birds are generally less philopatric and disperse greater distances than males (Greenwood 1980) and may thus be less likely to obtain benefits from prolonged philopatry. The results of my study, and the studies on

other species, suggest that delayed departure may have general benefits for the young of both cooperative and socially-monogamous species.

Although several studies have documented benefits to delayed dispersal, other studies have found that individuals that reduce the amount of time spent on their natal territory may also obtain benefits from early dispersal. Individuals that depart early sometimes travel shorter distances to vacant territories (Nilsson 1989) and can be more likely to recruit (Verboven and Visser 1998). Marsh tits that dispersed shortly following fledging benefited by acquiring a dominant position in a winter flock (Nilsson and Smith 1985, 1988) and moving shorter distances to find a breeding vacancy (Nilsson 1989). In dippers, departure shortly following fledging was commonly observed (45% departed before 12-14 days). Early departure does not appear to function by allowing access to high-quality wintering territories within the watershed or reducing the distance travelled to obtain a breeding vacancy. Few early-departing juveniles were resighted in their first winter or at recruitment age despite conducting this study at the watershed scale with multiple census sites separated by 2-5km and a detection distance of 0-40km. This suggests that these young may be travelling large distances. Dispersing juvenile Eurasian dippers are reported to move across drainages (Tyler and Ormerod 1994) suggesting that many juveniles in my study may be dispersing beyond my census area. Nevertheless, departure of young as soon as 6 days after nest departure, when provisioning rates remain high (see chapter 2), suggests that early departure may provide benefits to these individuals. Further work examining whether early dispersing young travel large distances and whether early and late dispersing young obtain benefits from differing dispersal strategies is warranted.

CHAPTER FIVE: CONCLUSIONS

The post-fledging period has received little attention despite the role that fledgling condition, foraging behaviour and timing of natal territory departure play in subsequent survival and lifetime reproductive success. In this study, I examined several aspects of fledgling and parental behaviour between nest departure and fledgling independence and the causes of variation in timing of natal departure. Specifically, I addressed patterns of food distribution during the post-fledging period, examined changes in mobility and foraging behaviour of fledglings and investigated the role of general intrinsic, environmental and behavioural factors in producing variation in timing of natal territory departure in American dippers.

In the first chapter, I examined the information content of fledgling begging and the use of begging for food allocation using behavioural observations of fledgling-parent interactions during the two-week post-fledging period. I asked whether fledgling begging expressed hunger or condition and whether the signal escalates in the presence of a sibling. I found that begging intensity was not influenced by the time between feeding events and so did not appear to reflect short-term hunger. I took advantage of inter-annual variation in provisioning rates to test the effects long-term need on begging. In the year with lower food delivery rates, begging intensities were higher suggesting that begging reflected long-term need. Next, I examined whether parents used begging cues when making allocation decisions and how parents respond to begging at the transition to independence. I found that patterns of food allocation were influenced by fledgling

begging. Both males and females, when presented with two fledglings in close proximity, followed the general decision rules of the nestling period, preferring to feed the closest- and most-intensively-begging fledgling. Parents changed their response to fledgling begging during the transition to independence. In the first week after fledging, parents were responsive to variation in begging returning sooner after high-intensity begging. In the second week, parents were no longer responsive to begging taking less time to return and no longer showing a response to variation in begging. I suggest that independence is influenced by changes in parental responsiveness to begging and departure decisions by individual fledglings. Fledgling condition was estimated using variation in food delivery rates thus was not measured directly. Given the role of fledgling condition in survival of juvenile birds, a further understanding of the patterns of food solicitation and allocation during the fledgling period is warranted.

In chapter three, I addressed patterns of fledgling foraging behaviour during the two-week dependant period using daily one-hour time budgets. I asked whether developmental or environmental constraints influenced foraging behaviour. I found that the foraging behaviour of male and female fledglings differed. Males integrated energetically challenging foraging behaviours into their repertoire sooner after nest departure than did females. Sex-specific differences in development were not explained by developmental or environmental constraints but may be reflective of differences in male and female natal departure decisions. I suggest that females may be selected to specialize on foraging behaviours that allow them to specialize on easily-captured prey types permitting early natal departure while males develop the full range of foraging behaviours seen in adults before they leave the natal territory. To understand the adaptive

role of this variation it would be important to explore the extent of the sex-differences in foraging tactics and microhabitat use into the first winter. Further work is warranted to explore the influence of sex-differences in behaviour on dispersal patterns, survival to recruitment and foraging patterns as a breeder.

In the fourth chapter, I investigated the causes of variation in timing of natal territory departure. I examined the roles of general intrinsic, environmental and behavioural factors on the timing of natal departure and began to examine the subsequent consequences of these decisions for survival to recruitment age. I used natal territory censuses to quantify timing of departure and long-term wintering-area censuses to address patterns of dispersal and local survival in this population. I found that timing of departure from the natal territory varied with 45% of birds with known departure times departing between 6-12 days after nest departure and 55% of birds remaining beyond 12-14 days. The sex and hatch date of fledglings had a greater effect on departure decisions than environmental factors or the behavioural phenotypes of individuals. Females and young born early in the season were the earliest to depart. I was unable to determine the consequences of early dispersal as none of these individuals were resighted at recruitment age. Males born early in the season and those that delayed departure were more likely to be seen at recruitment age. Since few young were resighted, I was not able to estimate survival probability and recruitment rates of females and early-dispersing young. Since natal dispersal decisions play a critical role in subsequent survival and lifetime reproductive success, investigation of the dispersal patterns of young from early broods and those that depart early are needed.

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