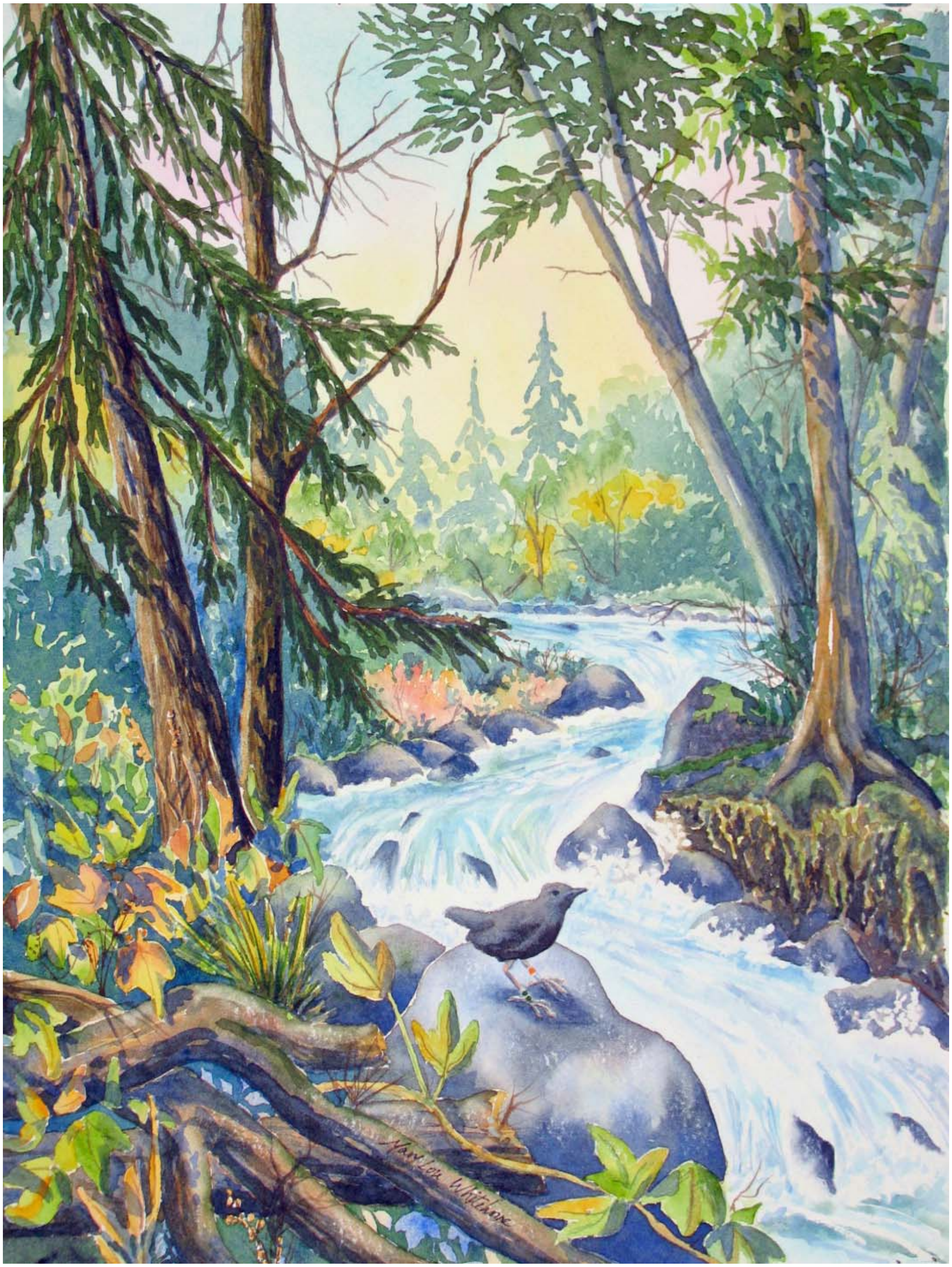

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MIGRATORY STRATEGY, REPRODUCTION AND SURVIVAL IN THE AMERICAN DIPPER, *CINCLUS MEXICANUS*

by

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BSc (Hons), Dalhousie University, 2005

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ABSTRACT

In some areas, populations of American dipper consist of altitudinal migrants and sedentary individuals that remain at low elevation year-round. Migrants have lower reproductive success due to later initiation of breeding, but also have higher annual survival than sedentary individuals (residents). I first evaluated whether age effects explain this difference in reproductive success. I then studied this apparent trade-off by evaluating if it is an expression of the cost of reproduction, and investigating if use of a multipurpose territory year-round restricted the foraging or site fidelity of residents during winter. Age effects do not explain the differences in reproductive success between migrants and residents. Additionally, there was no evidence that the greater reproductive effort of residents results in poorer physiological state that could negatively affect survival. However, migrants and residents differ in their fidelity to their wintering area, which may contribute to higher overwinter survival for migrants.

Keywords: Cost of reproduction; life history trade-off; survival; reproductive success; partial migrant; American dipper

Subject Terms: American Dipper; birds—ecology; birds—migration; birds—physiology; birds—reproduction

To my family, for all their endless love and support.

Most of all, to Dan. I couldn't have done it without you.

In memory of John Clydesdale Laird, 1924 - 2008

We miss you.

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ABBREVIATIONS

HY	Hatch year
AHY	After hatch year
SY	Second year
ASY	After second year
CV	Coefficient of variation
WBC	White blood cell
H:L ratio	Heterophil to lymphocyte ratio
TAC	Total antioxidant capacity
TOS	Total oxidative stress
PCA	Principal components analysis
PC1	Principal component 1
DW	Dry weight
WW	Wet weight

CHAPTER 1: GENERAL INTRODUCTION

Migration is a widespread phenomenon in birds, with half or more of all species exhibiting some form of migratory behaviour (Berthold 2001, Rappole 1995). Migration encompasses a wide range of behaviour, from annual movements between breeding and non-breeding areas than can span thousands of kilometres to short-distance altitudinal movements (Berthold 2001). Migration appears to have evolved independently in many lineages (Pulido 2007), and even multiple times within a single species (e.g. Pérez-Tris *et al*. 2004). There are several theories regarding the origins of migratory behaviour, such as forced movement due to changing climate, avoidance of seasonally poor conditions, tracking seasonal food resources, moving to take advantage of plentiful resources elsewhere, and avoidance of intraspecific competition (Rappole 1995). However, the processes underlying the evolution of this behaviour are still under debate (Bell 2000, Berthold 1999, Pulido 2007). A key step towards understanding the evolution of migration is understanding the costs and benefits of this behaviour.

One very common (Berthold 2001, Chan 2001, Rappole 1995) but poorly studied form of migration is partial migration, in which some individuals of a population migrate while others are sedentary (Terrill and Able 1988). Partial migration has been proposed to be a key step in the evolution of migration, as there is great potential for selective pressures can act on these populations to push them towards fully migratory or fully sedentary behaviour (Bell 2000, Berthold 1999, Pulido 2007). An understanding of partial migration is thus particularly important to understanding the evolution of migration. Partial migrants can be especially informative about the costs and benefits of migration, as migratory and sedentary individuals from the same population can be directly compared. This direct comparison avoids complications such as differences in phylogeny or habitat associated with comparing different species or populations.

I used a population of partially migratory American dipper, *Cinclus mexicanus,* to investigate the costs and benefits of migration. In partial migrant populations, migratory strategy can be genetically controlled (e.g. blackcaps *Sylvia atricapilla*, Berthold and Querner 1981), conditional, with subdominant individuals such as juveniles or females being more likely to migrate (masked weaver *Ploceus velatus*, Herremans 1994; blue tits *Cyanistes caeruleus*, Nilsson *et al.* 2008; Carolina junco *Junco hyemalis carolinensis*, Rabenold and Rabenold 1985; European blackbird *Turdus merula*, Schwabl 1983), or in some cases, both (e.g. European robin *Erithacus rubecula*, Adriaensen and Dhont 1990, Biebach 1983). While the mechanism that determines the migratory strategy a juvenile dipper will employ is not known, migratory strategy is largely fixed for life (less than 3% switch strategy, Gillis *et al*. 2008). This population is particularly well-suited for studying trade-offs associated with alternative migratory strategies, because comparisons between migratory and sedentary (resident) individuals can be made without concern for how costs and benefits change for an individual over their lifetime as they change migratory status. Additionally, gene flow between migrants and residents (Gillis *et al*. 2008) means the two groups are not genetically isolated.

Previous work on this population of dippers, located in the Chilliwack River watershed of southwestern British Columbia, has shown that migrants and residents differ in both reproductive success and survival. The higher reproductive success of the resident individuals appears to result from their earlier seasonal start to breeding, and consequently their greater probability of raising a second brood (Gillis *et al.* 2008, Morrissey 2004). Migrants thus pay a cost of migration in terms of reduced reproductive success, which is consistent with other reports of resident individuals breeding earlier or having higher reproductive success than migrants in other partially migratory populations (e.g. European robin, Adriaensen and Dhont 1990, European blackbird, Schwabl 1983). However, in this population migrants also appear to benefit from migration, as they have higher annual survival, though this higher survival does not completely offset the reduced reproductive success in terms of lifetime fitness (Gillis *et al.* 2008). The mechanism underlying this difference in survival rate, and thus how migrants benefit from migration, is unknown. In this thesis, I examine the apparent trade-off between survival and reproduction, and potential sources of the survival difference, to better understand the costs and benefits of migration.

Age is known to affect reproductive success in a wide variety of taxa (Clutton-Brock 1988, Sæther 1990) and this effect is very common in birds (Clutton-Brock 1988, Forslund and Pärt 1995, Martin 1995). Such age effects, which have not previously been assessed in this species, may have confounded apparent benefits of being sedentary if monitoring of reproductive success was biased with regards to age. In Chapter Two, I use an 8-year data-set to assess the effects of age on reproductive success in dippers, to determine if age effects could be contributing to the observed differences in reproductive success.

After assessing the potential effects of age on reproductive success, I address two hypotheses relating to the survival difference between migrant and resident dippers.

Firstly, I assess if the differences in reproduction and survival between the two strategies are an expression of the cost of reproduction. Increases in reproductive effort presumably carry a cost, such as reducing the number or quality of future offspring, and/or the probability of surviving to reproduce again in the future. This trade-off between current and future reproduction is called the “cost of reproduction” (Lessells 1991, Stearns 1989). In Chapter Three, I use a broad suite of physiological measures to assess if the lower reproductive effort of migrants, as a group, allows them to maintain a better physiological state at the end of breeding, which could in turn enhance their survival.

Secondly, I assess if the migrant-resident survival difference arises from differences in wintering behaviour. Winter is a harsh period for songbirds that remain in temperate regions, and it can be a period of high mortality. In my study population, resident dippers remain on their multi-purpose territory year round, while migrants maintain separate breeding and wintering areas. In Chapter Four, I assess if the use of such a multi-purpose territory (which must contain a nest site and thus may not be associated with the best winter feeding habitat), restricts the foraging behaviour or site fidelity of resident individuals in a way that could negatively affect their overwinter survival.

CHAPTER 2: AGE-DEPENDENT REPRODUCTIVE SUCCESS IN THE AMERICAN DIPPER

Abstract

Age is known to affect reproductive success in a wide variety of taxa. In birds, reproductive success typically increases with age in early life, before stabilizing and finally declining. Apparent age effects may result from improvement in the breeding performance of individuals or changes in the phenotypic composition of the breeding population, such as selective mortality of poor-quality individuals or delayed breeding of high-quality individuals. We used an information theoretic approach to evaluate models relating reproductive success to male and female age and migratory strategy in a partially migratory population of American dippers. We found support for an effect of female age (yearling vs. older) on reproductive success, and model-averaged parameter estimates indicate that yearling females produce on average 0.83 fewer fledglings than older females. There was less support for an effect of male age on reproductive success and little evidence that age effects varied with migratory strategy. Age related differences in the timing of reproduction, clutch size, fledging success and the number of breeding attempts all contributed to the difference in annual productivity between yearling and older females. We attempted to determine if the observed female age effects were due changes in the phenotypic composition of the breeding population or from individual changes in breeding performance by evaluating models relating annual productivity to survival in yearling females and by examining within-individual changes in breeding performance. We found evidence that yearling females that fledged fewer young were

less likely to survive to the subsequent year, indicating that selective mortality contributes to the female age effect. We found little to suggest that annual productivity improved with age within individual females, but sample sizes were small and prevented statistical evaluation of within-individual effects.

Introduction

Age has been found to influence reproductive success in a diversity of taxa, including insects, amphibians, mammals, and birds (Clutton-Brock 1988, Sæther 1990). In birds, reproductive success typically improves over the first few years of life before stabilizing and then declining in old age (Forslund and Pärt 1995, Martin 1995). This pattern of age-specific reproductive success may result from changes in breeding performance at the individual level, or changes in the phenotypic composition of the breeding population. Two hypotheses have been proposed to explain why individual birds may improve in reproductive success with age. First, young birds may initially perform worse than older birds because they forage less efficiently, are less skilled at detecting and avoiding predators or acquire lower quality territories or mates (constraint hypothesis, Curio 1983). Second, young birds may be capable of greater reproductive effort, but moderate their effort to optimize the trade-off between current and future reproduction and thus maximize lifetime reproductive success (restraint hypothesis, Curio 1983). Even if individual performance does not improve with age, mean reproductive success can increase with age if older age classes of breeding birds contain relatively more high quality individuals. This can occur if poor quality individuals, who have lower reproductive success, are less likely to survive (selective mortality hypothesis; Curio 1983, Forslund and Pärt 1995), or if high quality individuals defer reproduction in order to breed more successfully at an older age (delayed breeding hypothesis; Forslund and Pärt 1995, Hamann and Cooke 1987).

Empirical studies examining the mechanism leading to age-specific reproductive success have documented individual improvement in breeding performance across a wide variety of birds (e.g. passerines, Desrochers and Magrath 1993, Green 2001, Hatch and Westneat 2007, Wheelwright and Schultz 1994; falcons, Espie *et al*. 2000; seabirds, González-Solís *et al*. 2004; and rails, Perdeck and Cavé 1992), but few studies have been able to distinguish between the constraint and restraint hypotheses for within-individual improvement (but see Desrochers 1992). Studies have also evaluated whether age-related improvement in reproductive success results from changes in the phenotypic composition of breeding populations. Some studies provide support for the selective mortality hypothesis (see Forslund and Pärt 1995, and Reid *et al*. 2003 for reviews). Support for the delayed breeding hypothesis is rare, and typically has been observed only in long-lived species (e.g. northern fulmar *Fulmaris glacialis*, Ollason and Dunnett 1988; oystercatchers *Haematopus ostralegus*, van de Pol and Verhulst 2006). However, these four hypotheses are not mutually exclusive and several studies have shown that more than one mechanism can operate simultaneously (e.g. Espie *et al.* 2000, Low *et al.* 2007, Ried *et al*. 2003).

Age dependant patterns of reproductive success often vary between the sexes. In species where both sexes contribute to the rearing of the young, studies that have examined the independent effects of male and female age typically find that either both influence reproductive success (e.g. Espie *et al*. 2000, Hatch and Westneat 2007, Nol and Smith 1987, Wiktander *et al*. 2001), or that only female age does (e.g. Desrochers and

Magrath 1993, Low *et al*. 2007, Reid *et al.* 2003, but see Green 2001). In cases where both male and female age affect reproductive success, males and females often influence different aspects of breeding performance. For example, in brown thornbills (*Acanthiza pusilla*, Green 2001) female age influences laying date, while male age affects the probability of successfully fledging young and the proportion of fledglings that survive to independence. Similarly, in lesser spotted woodpeckers (*Dendrocopos minor*, Wiktander *et al*. 2001), laying date advances with female age but the number of young fledged increases with male age. The mechanisms by which age affects reproductive success can also differ between the sexes. In merlins (*Falco columbarius*), Espie *et al*. (2000) found that laying dates advanced and brood sizes increased with age for both males and females, but these effects were mainly due to within-individual improvement in males and selective mortality among females. Such differences between the sexes in patterns of age-dependant reproductive success may be related to the parental roles in each species. For example, if egg neglect is a significant contributor to hatching failure and both sexes incubate, then the age of both may affect hatching success. If only females incubate, however, male age would be expected to have less of an effect. Consequently, we may expect age effects of each sex to differ in species where the sexes have different roles, and to be more similar in species where males and females have similar roles.

Patterns of age-related reproductive success might also be expected to vary among species due to ecological or life history factors. Age could have a greater impact on breeding performance in species with particularly complex foraging methods (young birds may take longer to become proficient), territorial breeders (young, subdominant individuals may be forced into lower quality sites), or migratory species (young birds tend to arrive later, which subsequently affects reproduction). To date, no comparative studies have addressed how patterns of age-specific reproductive success vary between species in relation to ecological or life history factors. However, interactions between life history and age-specific reproductive success can be examined within a single species, if that species exhibits one or more alternate life histories. For example, partially migratory species can be used to investigate the interaction between migratory behaviour and age effects on reproductive success. Age effects may be more pronounced within migratory individuals, as it is well known that age affects arrival times in migratory species, and arrival time subsequently affects reproductive success (e.g. Lozano *et al.* 1996).

We used such a partially migratory species, the American dipper (*Cinclus mexicanus*), to investigate how patterns of age-related reproductive success varied between the sedentary and migratory fractions of the population. While age has been shown to positively affect brood size in the closely related white-throated dipper, *Cinclus cinclus* (Wilson 1996), the effects of age on reproductive success have not previously been described in American dipper, nor have interactions with other life history traits (such as migration) been considered. We used an 8-year data set to 1) simultaneously test for both male and female age effects on reproductive success, 2) examine if age effects vary with migratory strategy, 3) determine at what stage of the breeding cycle age-related differences occur, and finally 4) determine if age effects were due to within-individual improvement or selective mortality of poor quality individuals.

Methods

Study species and area

American dippers are relatively short-lived, socially monogamous passerines that show high levels of fidelity to their breeding sites (Middleton *et al*. 2006). Dippers exhibit biparental care, with both sexes contributing to nest construction and the care of nestlings and fledglings, though only females incubate and brood (Kingery 1996). Dippers typically re-nest if a clutch or brood is lost early in the breeding season, and may raise two broods a season. We have monitored a marked population of dippers in the Chilliwack River watershed, located approximately 100km east of Vancouver, British Columbia, Canada, since 1999 (for a detailed site description, see Morrissey *et al.* 2004). This population is composed of both altitudinal migrants and sedentary individuals (residents). Migrants overwinter with residents on the main stem of the Chilliwack River, but move to higher elevation breeding sites in the spring. Migrants typically have lower productivity (2.3 vs. 3.7 fledglings per year), but higher annual survival than residents (57.3 vs. 53.9 %, Gillis *et al*. 2008).

General methodology

Dippers were monitored throughout the breeding season (mid-March to early July) from 1999-2001 and 2003-2007. Breeding pairs were located by repeatedly searching all accessible sections of the river and tributaries on foot, checking suitable locations for nests, and following any dippers seen or heard. Pairs were observed at least weekly to determine incubation, hatch and fledging dates, and clutch and brood sizes of all nesting attempts. In some cases incubation and hatch dates were back-calculated using the nestling age when the nest was first checked, assuming incubation lasted 16 days

(Price and Bock 1983). When nests were inaccessible, nestling age was indirectly determined from repeated observations of begging behaviour, feeding rates, and size of prey items brought to the nest. This method was validated at nests where nestlings could be aged directly, and ages determined this way are considered accurate to within two days. If the brood successfully fledged (at least one fledging was observed) we assumed the number of fledglings produced was equal to the brood size at banding (10-14d old, see Morrissey 2004). In cases where brood size was unknown, the number of fledglings produced was determined by thoroughly searching the territory within two days of fledging. Any pairs where the total number of young fledged in a season could not be accurately determined were omitted from all analyses.

Sexing and aging

The sex of each breeding bird was determined behaviourally or by the presence or absence of a brood patch (only females incubate and brood; Kingery 1996). We classified all breeding birds as being yearlings (second year or SY), older (after second year or ASY), or of unknown age class. Birds were of known age class if they had been banded as a nestling (n = 24), or banded as an adult in a previous year (n = 139). Birds captured for the first time in 2006 and 2007 were classified as either SY or ASY based on the shape of the primary coverts and the presence or absence of a moult limit among the secondary coverts (n = 59; Pyle 1997). Birds that bred prior to 2006 were classified as SY if they replaced a banded bird on a territory and if there had been no unbanded birds of the same sex on adjacent territories in the previous year (n = 48). These birds are likely to be SY because dippers generally start to breed at one year of age, show a high fidelity to their breeding territories, and individuals that do disperse typically move to an adjacent territory (Middleton *et al*. 2006, Green, unpublished data). We evaluated this assumption using data from 2006 and 2007, where birds that replaced banded breeders and could not have come from adjacent territories (i.e. neighbouring birds of the same sex were all banded) were also aged using feather characteristics. All females that replaced a banded breeder were SY birds (n= 10). However, only 56% of males that replaced a banded breeder were SY (n = 9). Some ASY males may therefore have been misclassified as SY, which would reduce any apparent effect of male age on reproductive success.

Statistical methods

We restricted our analysis to the 88 breeding attempts where both male and female age could be assigned and the total number of young fledged over the season was known (Table 2.1). This sample included 33 individuals that were monitored in more than one year (range 1-4 years). Therefore we initially analyzed our data using mixed models with both male and female identity included as random terms. However, we found little variance associated with either identity term so we simplified the model structure by dropping the random terms (change in model deviance associated with dropping the female ID term full model = 0.000, χ^2 df = 1, p > 0.95; change in deviance associated with dropping the male ID term = 0.000, χ^2 df = 1, p > 0.95).

We subsequently used an information-theoretic approach to examine the effects of both male and female age on reproductive success, which was defined as the total number of young fledged per pair in a season. We compared nine general linear models using Akaike's Information Criterion, corrected for both small sample size (n = 88 pairs) and overdispersion ($\hat{c}$ = 3.26). The model set was selected to compare potential effects of male age and female age, as well as investigate interactions between male and female age, and age and migratory strategy (Table 2.2). In all models, we controlled for both migratory strategy and year effects, as these are known to affect reproductive success in this population (Gillis *et al*. 2008, Morrissey 2004). As our concern was identification of important variables rather than the best model *per se*, we used parameter likelihoods to assess the relative importance of each variable to reproductive success (Burnham and Anderson 2002), while model-averaged parameter estimates were used to assess the effect size and thus biological significance of each parameter. Parameter likelihoods, which are the sum of the Akaike weights of all models containing a given parameter, range from 0 to 1 and can be interpreted as the importance of each variable, relative to the other variables in the model set (Burnham and Anderson 2002). Model-averaged parameter estimates are parameters from a weighted-average model, which is calculated using the degree of support (Akaike weights, w_i) to determine the relative contribution of each candidate model in the set to the weighted-average model. The parameter estimates and associated standard errors from this weighted average model have reduced bias and incorporate model selection uncertainty (Burnham and Anderson 2002).

We then used a series of general linear models to examine how female age influenced performance during five stages of the breeding cycle. We only examined the influence of female age as our initial models provided greater support for an effect of female age on reproductive success than an effect of male age (see Results, Table 2.2, 2.3). Stages of the breeding cycle considered were: 1) timing of breeding, measured as the Julian date of the start of incubation of the first clutch, where January 1st = 1; 2) the size of the first clutch laid in a season; 3) hatching success, the proportion of eggs in each clutch laid that hatched; 4) fledging success, the proportion of eggs in each clutch that produced fledglings; and 5) the number of breeding attempts per season in which at least one egg was laid. In all analyses we controlled for effects of migratory strategy and possible effects of male age and annual variation. For analyses of clutch size, hatching success, fledging success, and number of breeding attempts, we also controlled for possible effects of the timing of breeding. Our estimate of hatching success is an underestimate of actual hatching success, as hatching success was determined at 10-14 days post-hatch and so combines hatching failure and early nestling loss. Clutches that were completely lost (e.g. predation, flooding) during incubation or prior to banding were excluded from the calculation of hatching success. The fledging success measure, however, includes all nests that failed at any time during incubation or the nestling period to reflect overall egg-to-fledgling success rates.

Finally, we assessed if the observed effect of female age on reproductive success resulted from selective mortality or within-individual improvement. If selective mortality contributed to the observed female age effect, the survival of yearling females from one breeding season to the next should be inversely related to their reproductive success, with those exhibiting low reproductive success being less likely to survive. To test for selective mortality, we used an information-theoretic approach to evaluate whether yearling females with greater reproductive success were more likely to survive until the subsequent breeding season (March of the following year). We compared four logistic regression models, using AIC corrected for both small sample size ($n = 29$) and overdispersion ($\hat{c} = 2.06$). The model set was selected to examine the effects of reproductive success and annual variation (year effects) on the survival of yearling females (Table 2.5). We used model-averaged parameter estimates to assess the impact of reproductive success on future survival. Effect sizes from logistic regressions are best expressed as odds ratios (the natural logarithm of the parameter estimate). Odds ratios are measures of relative risk, where risk is the probability of the event occurring divided by the probability of event not occurring. An odds ratio of 1 indicates no effect, while an odds ratio greater than one indicates increased risk. To test for individual improvement in reproductive success, we calculated the change in the starting date of incubation and number of offspring fledged by individual females from the first breeding season to subsequent seasons. We corrected for year effects by calculating relative start dates and reproductive success (the difference from the mean) within each year.

All means are presented ± 1 s.e. unless otherwise indicated. All analyses were run in GenStat 10th ed. (VSN International Ltd. 2007), and AIC values were calculated manually, after Burnham and Anderson (2002).

Results

Age and reproductive success

Two of nine models examining variation in reproductive success received strong support ($\Delta QAIC_C < 2$), with a further three models receiving moderate support ($\Delta QAIC_C < 4$, Burnham and Anderson 2002, Table 2.2). Female age was a factor in three of these supported models, including one of the strongly supported models. Male age appeared in two of the moderately supported models, as did a female age by strategy interaction (Table 2.2). While the model that received the most support (migratory strategy + year effects) did not contain any age terms, the second ranked model (which included female age) received essentially the same level of support as the first (w_i = 0.34 and 0.28 respectively).

Of the variables investigated in the model set, female age had the highest parameter likelihood (0.51), indicating that female age was of the greatest importance to reproductive success (strategy and year effects were included in all models to account for known effects and thus their parameter likelihoods were constrained to equal one). From the weighted-average model, yearling (SY) females were estimated to fledge 0.83 ± 0.92 fewer young than older (ASY) females (Table 2.3, Figure 2.1a). Male age had a considerably lower likelihood (0.26) and smaller effect, with young males estimated to fledge 0.17 ± 0.34 fewer young than older males (Figure 2.1b). A female age by migratory strategy interaction had a moderate estimated effect size, but a low likelihood (Table 2.3, Figure 2.1a). All other terms received negligible support.

Timing of the female age effect within the breeding cycle

Yearling (SY) females initiated incubation almost a week later than older (ASY) females, after controlling for known effects of migratory strategy, and potential effects of annual variation and male age (Table 2.4). Female age also had an effect on several other aspects of reproduction, after controlling for the earlier onset of reproduction in older birds. Yearling females laid smaller first clutches, had a lower fledging success per egg laid, and initiated fewer breeding attempts than older females (Table 2.4; controlling for effects of annual variation, migratory strategy, and male age). The only aspect of breeding in which yearling and older females did not differ was hatching success. Consequently, the female age effects detected in the previous analysis appear to result from age effects at multiple stages of the breeding cycle.

Evaluating the mechanism for female age effects

We first examined if reproductive success was related to survival in yearling females. Two models examining variation in survival of yearling females received considerable support ($\Delta QAIC_C < 2$, Table 2.5), while support for the remaining two models was negligible ($\Delta QAIC_C > 7$, Burnham and Anderson 2002). While the top ranked model ($w_i = 0.55$) indicated that survival was constant, the second ranked model, which included reproductive success, received a similar level of support ($w_i = 0.44$). The odds ratio calculated from the model-averaged parameter estimates indicate that a yearling female is 1.16 times more likely to survive for each extra fledgling she produces (Table 2.6). Alternately, the yearling females that survived until the subsequent breeding season fledged 3.3 ± 2.7 young (mean ± s.d., n = 11), while those that disappeared before their second breeding season fledged only 1.5 ± 1.9 young (mean ± s.d., n = 18, Figure 2.2). Our ability to assess whether an individuals' reproductive performance improved with age was limited, as we only had data on four females where the date of the incubation start was known as both a yearling and as an older bird, and seven females where their annual productivity was known both as a yearling and older. Given the limited dataset, there was no evidence that individuals' reproductive success improved with age, as four females increased the number fledged from yearling to older, and three decreased. The mean change (± 1 s.d.) in number of offspring fledged, corrected for year effects, was -0.05 ± 2.61. However, all four individuals advanced in the starting date of incubation from yearling to older, suggesting that a larger sample may reveal trends for within-individual improvement in reproductive performance. The mean advancement (±1 s.d.) in the start of incubation from one season to the next, corrected for year effects, was 11.3 ± 4.9 days.

Discussion

Breeding performance typically increases with age in birds in early life, before stabilizing and finally declining (Forslund and Pärt 1995, Martin 1995). The extent to which breeding performance improves with age may differ between the sexes, particularly if the sexes differ in their parental roles or on their contribution to raising the young. Changes in breeding performance with age may also be expected to differ among species in relation to their life histories. For example, age may have a more pronounced effect in migratory species, as young birds tend to arrive on the breeding grounds at a later date, and later-breeding individuals tend to have lower reproductive success (e.g. Balbontín *et al*. 2007, Lozano *et al.* 1996). Species with multiple life history strategies, such as the American dipper, offer an opportunity to explore interactions between life history traits such as migration and patterns of age-related reproductive success. Our results were somewhat surprising in that female age was found to have a greater impact on reproductive success than male age, despite the sexes having similar roles, and that we found no difference in the patterns of age-related improvement in reproductive success between migratory and sedentary American dippers.

Our analyses suggest that female age has a larger role than male age in determining annual productivity in dippers. This was somewhat unexpected as both male and female dippers contribute to most activities associated with breeding, and only incubation and brooding of young is carried out exclusively by one sex (the female; although males may feed incubating/brooding females, Kingery 1996). However, this is consistent with the many studies that have examined the independent effects of male and female age, which typically find that breeding performance is affected either by the age of both sexes or by female age alone (e.g. Balbontín *et al.* 2007, Desrochers and Magrath 1993, Espie *et al*. 2000, Hatch and Westneat 2007, Low *et al*. 2007, Nol and Smith 1987, Reid *et al.* 2003, Wiktander *et al*. 2001). The dominance of the female age effect may be because one of our aging methods (the assumption that individuals replacing banded breeders were yearlings) was less accurate for males, which may have resulted in some older males being misclassified as yearlings (see Results). Such misclassifications would reduce any apparent effect of male age on reproductive success. However, only about half of males classified as yearlings (SY) were aged using the less accurate method (n = 16 of 28 SY males; the remainder were banded as nestlings or aged by feather characteristics). All males classified as ASY (n = 60) were either banded as nestlings, banded as adults in a previous year, or were aged on the basis of feather characteristics. Assuming that about half of the males that replaced banded breeders (n = 16) were misclassified (44% error rate, see Results), we can estimate that only about 8 of the total of 88 males used in the analysis were incorrectly aged. While this would bias the results towards underestimating the effects of male age, it seems unlikely that a misclassification rate of about 10% would completely mask any effect of male age on reproductive success. Alternatively, female age may have a greater effect on reproductive success than male age because female birds have greater control than males over some aspects of the breeding cycle, such as the timing of breeding (e.g. Caro *et al.* 2009). In the dipper, female age impacts a number of aspects of breeding, most of which are related to egg production and are presumably under female control. If overall age-related differences in reproductive success originate in these female-controlled stages, as they appear to in the dipper, the effect of female age would consequently be greater than that of male age.

In dippers, we expected that age effects would be more pronounced in migrant individuals, as the reproductive success of young migrants may be reduced due to delayed arrival on the breeding site, in addition to any other effects of age experienced by both resident and migrant individuals. However, while we did find that female age affected reproductive success, we found no evidence that this age effect was more pronounced in migrants. Migratory strategy may not influence patterns of age-specific reproductive success in dippers because dippers migrate only short distances (2 - 21 km, Gillis *et al*. 2008), which may not be far enough for age to significantly affect the timing of arrival at a breeding area. Interactions between migratory strategy and patterns of age-specific reproduction may be more pronounced in partial migrants that travel longer distances. Alternatively, age effects may not have varied with migratory strategy because any effect of slow migration or delayed arrival at the breeding site may have been masked by more general age effects, as female age was found to affect a number of aspects of breeding performance other than the onset of breeding.

Overall patterns of age related reproductive success in birds can arise through improvements at many different stages of the breeding cycle, from the timing of arrival on the breeding grounds (e.g. Lozano *et al*. 1996) through rearing fledglings to independence (e.g. Green 2001), and improvements can occur at multiple stages simultaneously (e.g. Balbontín *et al*. 2007, Green 2001, Reid *et al* 2003). Improvements in reproductive performance associated with age in female dippers appear to occur at most stages of the breeding cycle. Like many other birds, older female dippers begin breeding, on average, earlier than young females. Earlier breeding dippers tend to have higher reproductive success, due to a combination of fewer losses to predation and flooding, and increased likelihood of a second brood (Morrissey 2004). After controlling for date effects, older female dippers also lay larger first clutches, have higher fledging success, and undertake more breeding attempts per season. Only hatching success was not significantly affected by female age.

Selective mortality has not been supported in empirical studies as often as within-individual improvements (reviewed in Forslund and Pärt 1995, Martin 1995, and Reid *et al*. 2003), and some studies have even found that individuals that produce more young in a season are less likely to survive (Desrochers and Magrath 1993, Dow and Fredga 1984, Pugesek 1987). However, the increase in reproductive success with age in female dippers appears to be due, at least in part, to selective mortality. While the top ranked model indicted that survival of yearling female dippers was constant, the second-ranked model, relating probability of survival to reproductive success, received essentially equal support, indicating that both models fit the data well, with little to distinguish the two. It is not surprising that the model indicating constant survival received the top ranking, as the sample size was small and AIC rankings penalize models containing more parameters (Burnham and Anderson 2002). It is therefore important to recognize that the model relating survival to reproductive success received substantial support ($QAIC_C > 2$, $w_i = 0.44$), and far more support than the remaining models (Table 2.5). The yearling females that survived until the following year fledged substantially more young during their first breeding attempt than the yearlings that disappeared, indicating that reproductive success and survival are positively correlated. This is consistent with the argument that selective mortality may be more likely to account for age-related improvements in reproductive success in short lived species with high annual mortality (Forslund and Pärt 1995).

However, selective mortality has been found across a diversity of taxa, including long-lived birds with low annual mortality (Barbraud and Weimerskirch 2005, Mauck *et al.* 2004, and reviewed in Reid *et al.* 2003), and studies have looked for but failed to find evidence of selective mortality across an equally diverse range of birds, again including both short and long lived species (passerines, 9 spp; ducks and geese, 5 spp; seabirds, 1spp; reviewed in Reid *et al.* 2003). This suggests that there is no simple relationship between lifespan, annual mortality, and the likelihood of selective mortality playing a role in the effects of age on reproductive success.

Most studies investigating the mechanisms underlying the effects of age on reproductive success find that within-individual improvement plays a role. In contrast, we did not observe any evidence for an increase in the number of young fledged in female dippers from their first to subsequent breeding seasons, though individuals may advance the date of the start of incubation. However, our sample was very small and the possibility of improvement in breeding performance within individual female dippers needs to be investigated with additional data.

Delayed breeding can lead to an apparent effect of age on breeding performance, if high quality individuals begin breeding at an older age than poorer quality individuals (Forslund and Pärt 1995, Hamann and Cooke 1987). Such deferral may be beneficial if, for example, the delaying individuals are queuing for high-quality territories (Ens *et al.* 1995). Although not directly evaluated in this study, we do not believe delayed breeding plays a role in patterns of age-specific reproductive success in the dipper. Firstly, dippers are short lived (annual survival 54-57%, Gillis *et al.* 2008), and the costs of skipping a breeding season should far outweigh any potential benefits of queuing for a better quality territory. Secondly, over 90% of individual dippers banded as nestlings that recruited into our study population were found breeding at one year of age (n= 23, 1 individual was omitted as it was found breeding at 5 years of age in an area that had not previously been monitored). Variation in age at first reproduction in dippers is therefore very low and unlikely to be a significant contributor to apparent age-dependent changes in reproductive success.

In summary, we found that in American dippers, female age has greater effect on reproductive success than male age, with older females fledging more young than yearlings. These age effects did not vary with migratory strategy in this partially migratory population, suggesting that age effects are unlikely to explain previously observed differences in the reproductive performance of residents and migrants in this system (Morrissey 2004, Gillis *et al*. 2008). Female age was found to affect multiple stages of the breeding cycle, including timing of breeding, first clutch size, fledging success, and the number of breeding attempts undertaken in a season. This pattern of age-related reproductive success appears to result, at least in part, from selective mortality of poor-quality individuals.

Table 2.1: Age structure of pairs of breeding American dippers used to analyze effects of age on reproductive success.
N = 88 pairs, consisting of 66 unique males, 69 unique females, and 81 unique pairs. SY= second year, ASY = after second year.

Number of Breeding Pairs			
		Male Age	
		Yearling (SY)	**Older (ASY)**
Female Age	**Yearling (SY)**	15	21
	Older (ASY)	13	39

Table 2.2: General linear models relating reproductive success to parental age in American dippers. Model parameters: RS, reproductive success; S, migratory strategy (resident or migrant); Y, year; F, female age (SY or ASY); M, male age (SY or ASY); * denotes an interaction term. Table headings: k, number of parameters estimated in the model; $\Delta QAIC_C$, the difference between a given model's $QAIC_C$ and the lowest $QAIC_C$; w_i, Akaike weights. Pearson's r^2 is included as a measure of model fit. n = 88 breeding pairs for all models.

Model	**k**	**$QAIC_C$**	**$\Delta QAIC_C$**	**w_i**	**r^2**
RS = S + Y	10	71.84	0.00	0.34	0.11
RS = S + Y + F	11	72.23	0.38	0.28	0.19
RS = S + Y + M	11	74.02	2.18	0.12	0.13
RS = S + Y + F + F*S	12	74.06	2.22	0.11	0.21
RS = S + Y + M + F	12	74.71	2.87	0.08	0.19
RS = S + Y + M + M*S	12	76.70	4.86	0.03	0.13
RS = S + Y + M + F + M*F	13	77.25	5.41	0.02	0.20
RS = S + Y + M + F + M*S + F*S	14	79.36	7.52	0.01	0.22
RS = S + Y + M + F + M*S + F*S + M*F + M*F*S	16	84.69	12.85	0.00	0.24

Table 2.3: Parameter likelihoods and parameter estimates from the weighted-average model of age effects on reproductive success.
Likelihoods of the intercept, strategy term and year terms are all constrained to equal one as these terms are included in all models of the set (see Table 2.2). Terms in brackets indicate the associated parameter likelihood and s.e. is for that level of a categorical variable; e.g. (SY) means the associated coefficient is the effect of being SY as compared to ASY. Parameter notation is the same as Table 2.2.

Parameters	**Parameter Likelihood**	**Weighted Parameter Estimate**	**Unconditional Standard Error**
Intercept	1.00	3.76	0.93
S (migrant)	1.00	-1.59	0.81
Year	1.00	-	-
(2000)	-	1.30	1.11
(2001)	-	0.20	0.97
(2003)	-	1.14	1.06
(2004)	-	-0.99	1.21
(2005)	-	-0.46	1.24
(2006)	-	0.29	0.96
F (SY)	0.51	-0.83	0.92
M (SY)	0.26	-0.17	0.34
F*S (SY*migrant)	0.12	0.31	0.61
M*S (SY*migrant)	0.04	0.00	0.07
F*M (SY*SY)	0.00	0.02	0.06
F*M*S (SY*SY*migrant)	0.00	0.00	0.00

Table 2.4: Breeding performance of yearling (SY) and older (ASY) female American dippers at different stages of the breeding cycle.

Values are expressed as least squared means ± s.e., and were calculated while controlling for effects of migratory strategy (S), and possible effects of male age (M), year effects (Y), and timing of breeding (date of start of incubation of the 1st clutch, D), when applicable. Sample sizes vary because not all information was available for all nests. Asterisks indicate statistical significance of terms controlled for in the models (*p < 0.1, **p < 0.05, ***p < 0.01).

	SY	**n**	**ASY**	**n**	**t**	**p**	**Controlling for:**
Date of incubation start	97.2 ± 2.1	36	90.9 ± 1.7	52	2.30	0.02	S^{*}, M, Y^{***}
First clutch size	4.1 ± 0.2	16	4.6 ± 0.1	42	-2.41	0.02	S^{***}, M, Y, D
Hatching success	0.87 ± 0.05	13	0.80 ± 0.03	56	1.00	0.25	S, M, Y^{***}, D
Fledging success	0.50 ± 0.06	19	0.68 ± 0.03	67	-2.50	0.01	S, M, Y^{***}, D
Number of attempts	1.3 ± 0.1	36	1.6 ± 0.1	52	-2.45	0.02	S, M, Y, D

Table 2.5: Logistic regression models linking survival of yearling females to reproductive success, including year effects.
Model parameters: RS, reproductive success; Y, year. N = 29 yearling females; 11 survived to the next breeding season and 18 disappeared. Migratory strategy was not included in the models due to inadequate migrant sample size (n = 3). Nagelkirke's r^2, a logistic-regression equivalent of Pearson's r^2, is included as a measure of model fit. See Table 2.2 for details of table headings.

Model	**k**	**$QAIC_C$**	**$\Delta QAIC_C$**	**w_i**	**Nagelkirke's r^2**
Survival = Constant	1	20.87	0.00	0.55	-
Survival = RS	2	21.33	0.46	0.44	0.17
Survival = Y	6	31.97	11.10	0.00	0.23
Survival = RS + Y	7	32.07	11.20	0.00	0.47

Table 2.6: Parameter likelihoods, parameter estimates and odds ratios from the weighted-average model of yearling female reproductive success and survival.

Parameters	**Parameter Likelihood**	**Weighted Parameter Estimate**	**Unconditional Standard Error**	**Odds Ratio**
Intercept	1.00	-0.85	1.25	-
Reproductive Success	0.44	0.15	0.28	1.16
Year	0.00	-	-	-
2000	-	0.00	0.93	1.00
2001	-	0.01	0.91	1.01
2003	-	-0.08	12000	0.92
2004	-	0.00	1.00	1.00
2005	-	0.01	1.17	1.01

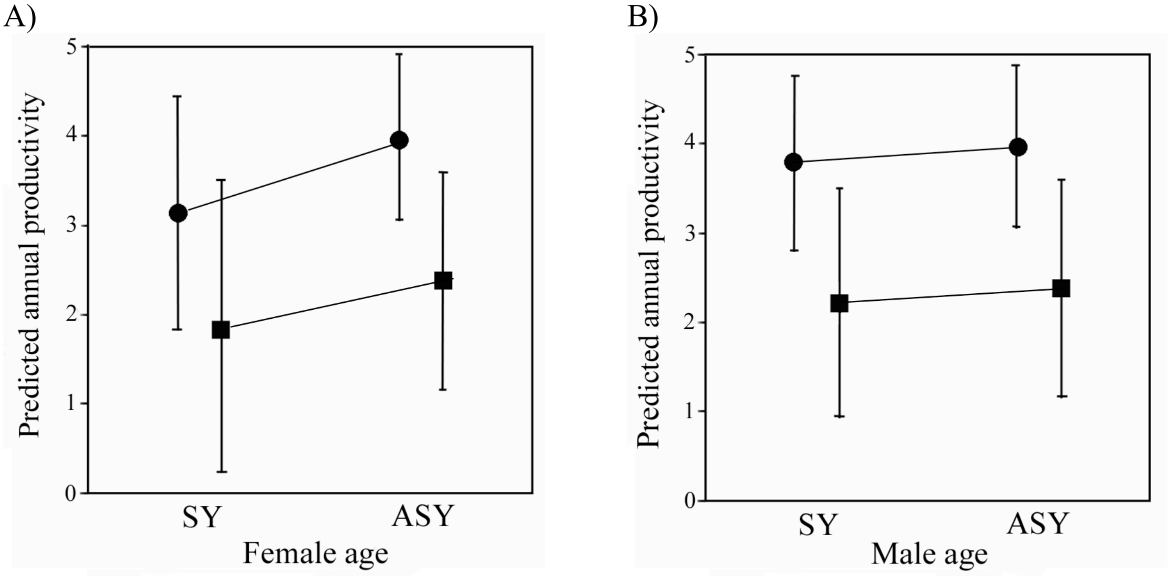

Figure 2.1: Predicted annual productivity of American dippers in relation to age.
A) females. B) Males. Annual productivity is expressed at the total number of young fledged during the breeding season. Age is expressed as SY (yearlings) versus ASY (older). Predictions are made from the weighted-average model of age and productivity (see Table 2.3 for model-averaged parameter estimates) and presented ± 1 s.e. Residents are represented by filled circles and migrants by filled squares.

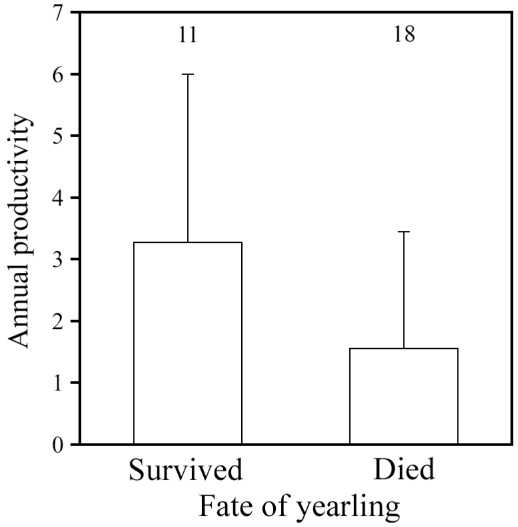

Figure 2.2: Annual productivity of yearling female American dippers in relation to subsequent survival. Annual productivity is expressed as the total number of young fledged. Yearling females were either known to have survived until the subsequent breeding season, or disappeared and are assumed to have died. Numbers indicate sample size in each category. Error bars represent 1 s.d.

CHAPTER 3: MIGRATORY AND SEDENTARY AMERICAN DIPPERS DO NOT DIFFER IN PHYSIOLOGICAL STATE AT THE END OF BREEDING

Abstract

The cost of reproduction (the trade-off between current and future reproduction) is one of the most-studied life history trade-offs, but the physiological mechanisms underlying this trade-off remain poorly understood. Recently, both immune system function (theorized to be energetically costly) and oxidative stress (an unavoidable byproduct of metabolism) have been hypothesized to underlie the physiological trade-off between current and future reproduction. The cost of reproduction has typically been investigated within individuals by experimentally manipulating reproductive effort and evaluating any resulting physiological changes in the manipulated individuals. An alternative to this individual-based experimental approach is to compare populations or groups that naturally vary in their reproductive effort. We used this comparative approach to investigate an apparent trade-off between reproduction and survival in the American dipper. In mountainous areas, dipper populations are partially migratory, consisting of altitudinal migrants and sedentary (resident) individuals. The two migratory strategies appear to be trading off reproductive effort and survival, as migrants have significantly lower productivity, but higher annual survival. If the lower reproductive effort of the migrants, as a group, is facilitating their higher survival, we expected that at the end of breeding migrants should show signs of better physiological state that could lead to enhanced survival. We evaluated this hypothesis by measuring a broad suite of physiological measures relating to several aspects of health, including immune system function and oxidative stress, in unmanipulated birds of both migratory strategies at the end of breeding. We found no evidence that migrant and resident dippers differ in physiological state at the end of breeding. Similarly, none of the ten physiological measures were significantly correlated with either short- or long-term workload (after Bonferroni correction for multiple comparisons). We found no differences between migrants and residents to support either the immune system or oxidative stress hypotheses. These results indicate that migrants and residents are in similar health at the end of breeding, and migrants are not gaining a physiological benefit from their lesser reproductive effort. Consequently, there is no evidence that the difference in survival between the two groups is caused by physiological consequences of the difference in reproductive success.

Introduction

Understanding the evolution of life histories requires an understanding of the trade-offs between life history traits. Life history trade-offs can be revealed using cross-species comparisons (e.g. Badyaev and Ghalambor 2001, Warne and Charnov 2008), but trade-offs also occur within individuals, as individuals vary in how they allocate limited resources between potentially competing life history traits (Stearns 1989). A classic life history trade-off is that between current and future reproduction. Theory predicts that this trade-off arises because increasing the current reproductive effort imposes a cost on the reproducing organism, by reducing the number or quality of future offspring, and/or the probability of surviving to reproduce again in the future (Lessells 1991, Stearns 1989). This “cost of reproduction” is often difficult to directly observe at the individual level, because variation in quality between individuals can mask the trade-off between current and future reproduction within individuals (Reznick *et al*. 2000, van Noordwijk and de Jong 1986). A high-quality individual with many resources can devote more resources, in absolute terms, to both self-maintenance and the current reproductive effort than a poor-quality individual with few resources can, leading to an apparent positive correlation between current and future reproduction (van Noordwijk and de Jong 1986). Consequently, experimental manipulation of reproductive effort, parental quality, or total resource availability is often required to observe the cost of reproduction at an individual level.

Although the cost of reproduction is one of the most studied trade-offs in life history theory (Harshmann and Zera 2007, Lessells 1991, Williams 1966), the mechanisms underlying this trade-off remain poorly understood (Harshmann and Zera 2007). The cost of reproduction may be mediated by ecological mechanisms, such as increased predation risk or greater use of hazardous areas with increasing reproductive effort (Lessells 1991). The cost of reproduction may also be mediated by physiological mechanisms, generally thought to result from the fact that limited resources must be divided between both self-maintenance and the breeding effort (Harshmann and Zera 2007, Lessells 1991). However, the cost of reproduction is often expressed long after the current breeding effort has ended. For example, increasing current reproduction may increase mortality during the following winter (Visser and Lessells 2001) or subsequent years (Orell and Belda 2002), or decrease future fecundity (Gustafsson and Sutherland 1988), and the mechanisms that would allow effects to persist over such time spans remains elusive.

One recently proposed long-term physiological mechanism is that investment in reproduction compromises the immune system of an individual (Sheldon and Verhulst 1996). Reduced immunocompetence is then expected to lead to increases in disease and parasitism, a loss of condition, and reduced survival (Deerenberg *et al.* 1997, Gustafsson *et al*. 1994, Moreno *et al.* 1999, Nordling *et al.* 1998, Ots and Hõrak 1996, Saino *et al.* 1997a). A second potential long-term physiological mechanism that has received recent attention is cellular damage caused by reactive oxygen species or other free radicals. The production of free radicals, which can damage many parts of cellular structure, is an unavoidable byproduct of mitochondrial respiration and increases with increased metabolic activity (Finkel and Holbrook 2000). Oxidative stress, the imbalance between free radical production and their removal by antioxidant defences, has been shown to increase with reproductive effort in birds (Alonso-Alvarez *et al.* 2004, Wiersma *et al.* 2004). The damage from such oxidative stress is thought to be cumulative over a lifetime, and has been implicated in age-related diseases and senescence (Finkel and Holbrook 2000, Muller *et al*. 2007), which could in turn impair future reproduction.

In birds, attempts to determine the physiological mechanism underlying the cost of reproduction usually rely on an experimental approach. This is often done by experimentally enlarging or reducing clutch or brood sizes, and then observing if the altered reproductive effort results in physiological changes in the individuals whose breeding effort has been manipulated. Other studies addressing the immune system hypothesis have done the reverse by manipulating the immune system and observing the effect on reproductive performance. These experimental studies have provided support for both the immune system and oxidative damage hypotheses (Alonso-Alvarez *et al.*

2004, Moreno *et al.* 1999, Nordling *et al*. 1998, Ots and Hõrak 1996, Tomas *et al*. 2007, Wiersma *et al.* 2004). However, results can be contradictory, with similar studies failing to find similar effects (e.g. Ilmonen *et al*. 2000 and Williams *et al.* 1999a). Additionally, the utility of experimentally enlarging and reducing broods or clutches has been questioned, as these manipulations ignore the earlier stages of the reproductive cycle, such as egg production (Monaghan and Nager 1997).

An alternative to experimental manipulation of the reproductive effort of individuals is to compare populations or subpopulations that differ in their reproductive effort. Reproductive effort can vary considerably with latitude in widespread species such as house wrens (*Troglodytes aedon*, Young 1996) house sparrows (*Passer domesticus*, Martin *et al.* 2004), and yellow warblers (*Dendrioca petechia*, Salgado-Oritz *et al*. 2008). Populations such as these can serve as "natural experiments," as the differences in life histories between groups are all different solutions to the problem of allocating resources between conflicting needs while attempting to maximize fitness in each particular environment. Investigation of how varying levels of reproductive effort between these groups influence a broad suite of physiological measures, including immune system function and oxidative stress, may shed light on the physiological mechanisms underlying the cost of reproduction.

We used this comparative approach to investigate if an apparent trade-off between reproduction and survival in the American dipper (*Cinclus mexicanus*) is an expression of a physiologically-mediated cost of reproduction. Dippers are suitable for this approach because populations in mountainous areas are composed of individuals that exhibit one of two alternate life histories (altitudinal migrant vs. sedentary individuals). The migratory individuals have significantly lower reproductive success, but higher annual survival (Gillis *et al*. 2008, Morrissey 2004). Additionally, the migratory and sedentary (resident) fractions of the population live in close contact, which avoids many environmental confounds (such as day length, temperature, food availability and habitat type or quality) associated with comparing populations across latitudes or other large distances. As migrants have a shorter breeding season than residents, they are less likely to raise a second brood (Gillis *et al*. 2008, Morrissey 2004). Because of this reduced reproductive effort, migrants may have more resources available to devote to self-maintenance than residents, and potentially enhance their annual survival rates. We used a broad suite of physiological measures to assess the overall health of breeding dippers to determine if the reduced reproductive effort of migrants is associated with enhanced physiological state at the end of breeding, and if these effects were more closely associated with oxidative stress or function of the immune system. We also assessed the extent to which short-term physical workload (distance flown per hour to provision the young) and long-term reproductive workload (the total number of offspring raised) influence the physiological state of the individual.

Methods

Study species and site

Dippers are mid-sized (ca. 50-55g) aquatic passerines that inhabit steep mountain streams and rivers. Dippers are socially monogamous and exhibit biparental care, with both sexes contributing to nest construction and the care of nestlings and fledglings.

Dippers will typically re-nest if a clutch or brood is lost early in the breeding season, and may raise up to two broods per season.

We have studied a marked population of migratory and sedentary dippers in the Chilliwack River watershed, approximately 100km east of Vancouver, British Columbia, Canada, since 1999 (for a detailed site description, see Morrissey 2004). Migratory individuals have a consistently lower annual fecundity, producing on average 1.4 fewer fledglings per pair per year than resident birds. This difference in reproductive success appears to be traded-off with survival, as the migratory individuals also exhibit an approximately 4% higher annual survival rate (Gillis *et al*. 2008).

Determining long-term reproductive workload

We monitored approximately 30 breeding pairs per year throughout the breeding seasons of 2006 and 2007. Breeding pairs were found by searching all accessible sections of the river and tributaries on foot, while checking potential nesting sites such as cliffs, undercut banks, midstream boulders, and bridges, and by following any dippers seen or heard. Breeding pairs were classed as sedentary if they occupied breeding territories on or within 1km of the main stem of the Chilliwack River, and were observed in the same area during fall and winter (n= 40 resident pairs). Pairs were classified as altitudinal migrants if they occupied breeding territories on creeks more than 1 km from the main stem of the river were not observed on these territories in winter (n = 17 migratory pairs).

All breeding pairs were monitored every 2-7 days throughout the breeding season (April to June) to determine the onset of incubation, hatch, and fledging dates associated with all breeding attempts, and the total number of young fledged. Nests were visited to determine clutch and brood sizes if access was possible. Precise clutch and incubation initiation dates were calculated from either observed laying dates, or were back-calculated from the age of the nestlings, assuming an incubation period of 16 days (Price and Bock 1983). For nests that could not be directly accessed, nestling age was estimated based on when the parents were first observed to provision young, the size of food items taken to the nest, the time taken to deliver food to the young, and the volume of nestling begging. This method was validated using nests where the exact age of the nestlings was known, and nestling ages determined this way are considered accurate within two days. For nests that successfully fledged at least one young, the total number of fledglings was assumed to equal brood size at banding (n = 24 broods, Morrissey 2004). If brood size was unknown, the number fledged was determined by thoroughly searching the territory within two days of fledging and counting the young (n = 20 broods). An additional 21 nesting attempts failed to fledge any young.

Measuring short-term parental workload

Short-term parental workload was measured as the distance flown per hour by adult birds when provisioning young. Short-term workload was measured during the last week of the nestling phase (nestlings 18 to 23 days old) during a 30 min (2006) or 60 min (2007) observation period. During these observations, we recorded the total number of times parents delivered food to the nest, and, where possible, the identity of the parent delivering food. Broods were fed 14.9 ± 7.8 times per hour (n = 43). A second observer recorded the distance parents travelled to gather food using a laser rangefinder (Bushnell Yardage Pro Sport). Provisioning distances were obtained for as many trips as possible during the observation period, with a minimum of four (in 2006) or six (in 2007) flight distances recorded for each breeding pair. Typical flight distances were less than 300m, and the mean distance of all flights recorded was 98 ± 80 m (n = 284 flights). Occasionally (21 of 284 observations) birds flew further than they could be tracked. In these cases we recorded the distance from the nest to the furthest location at which the bird had been observed, which introduces some bias by truncating the longest distances flown. In all cases, however, these birds returned within minutes and presumably did not forage at substantially greater distances then where they were last observed. Flight distances of both sexes were pooled due to the difficulty of identifying birds in flight. Parental workload was then calculated as the number of trips each individual undertook per hour multiplied by the average round-trip distance flown by that pair, and expressed as kilometres flown per hour. Parental workloads ranged from 0.16 to 5.09 km flown per hour.

Survival

We assessed within-breeding season and annual survival rates as part of regular monitoring of all breeding pairs. Individuals that initiated a breeding attempt (i.e. laid ≥ 1 egg) were classified as surviving the breeding season if they fledged young or, if their breeding attempt failed, were observed after the failure event. Individuals were classified as having died if they disappeared before the brood was due to fledge and were not found during at least two extensive surveys of the territory shortly thereafter. Individuals that initiated a breeding attempt in 2006 and 2007 were considered to have survived the year if they were resighted between April and June of the following year. All sites and adjacent areas used as a breeding site in one year were monitored regularly in the subsequent year.

Assessing physiological state

We used a broad suite of physiological measures to determine the physiological state of breeding adults late in the breeding season when breeding-induced declines in physiological state are expected to be most visible. Ten measures relating to four different aspects of health were assessed: general condition measures (size-corrected mass and hematocrit), immune system function (leucocrit, total white blood cell count, the ratio of heterophils to lymphocytes, and immunoglobulin levels in peripheral blood), metabolism of lipid stores (levels of circulating triglycerides and free glycerol), and oxidative stress (total antioxidant capacity and total oxidative status of blood plasma). We provide some context for these measures below.

Size-corrected mass reflects the size of a bird's fat stores or muscle mass, and has often been used as a general measure of condition. Body mass can decrease with increased workload during breeding (Moreno *et al*. 1999), and over time during the breeding cycle (Dawson and Bortolotti 1997). This mass loss may be due to stress (Suárez *et al*. 2005) or may be deliberately shed to improve flight performance (Cichon 2001, Norberg 1981).

Hematocrit, the volume of blood consisting of red blood cells, can be lowered by blood loss, parasitism, disease or severe nutritional stress (Dein 1986, Piersma *et al*. 2000), and elevated hematocrits can arise as a beneficial adaptation to the increased oxygen demands of a high workload (Hõrak *et al*. 1998, Saino *et al*. 1997b).

Leucocrit, the volume of blood consisting of white blood cells (WBC), and the *total white blood cell count* are both indicators of the level of activity of the immune system, though the two measures are often only poorly correlated to one another (Ots *et* *al*. 1998, Smits and Williams 1999). Infections and stress can increase the quantity of WBC in circulation (Rose *et al*. 1979, Smits and Williams 1999), and the quantity of WBC has been found to be negatively correlated to breeding performance (Gustafsson *et al*. 1994, Moreno *et al*. 1998).

The *ratio of heterophils to lymphocytes* (two common types of white blood cells) has long been used as a measure of stress in poultry (Gross and Siegel 1983) and is now often used as a reliable indicator of stress in other birds (including ecological studies of free-living populations; Hõrak *et al*. 1998, Moreno *et al*. 1998, Ots and Hõrak 1996) and many vertebrate taxa including mammals, reptiles and fish (Davis *et al*. 2008). A diverse range of stressors have been shown to both increase heterophil (neutrophil) numbers and decrease lymphocyte abundance in the peripheral blood, and indicates suppression of immune function (Dhabhar *et al*. 1995, Gross and Siegel 1983, Smits and Williams 1999).

Plasma immunoglobulins are another indicator of the level of activity of the immune system. Immunoglobulin levels can rise in response to parasites or infection, but levels are also thought to reflect the capacity of the immune system to mount a response (Morales *et al*. 2004).

The level of *triglycerides* in blood plasma is indicative of the rate at which the individual is fattening, while *free glycerol* is indicative of fat being metabolized (Guglielmo *et al.* 2005, Schaub and Jenni 2001, Williams *et al*. 1999b). These measures reflect the nutritional state of an individual for a period ranging from hours to a few days pre-sampling (Jenni-Eiermann and Jenni 1994, Williams *et al*. 1999b).

Total antioxidant capacity (TAC) refers to the overall ability of a fluid (such as blood plasma) to reduce potentially damaging oxidants, including the additive or interactive effects of the various antioxidant compounds present (Erel 2004). A higher antioxidant capacity reflects a greater ability to remove oxidants. *Total oxidative status* (TOS) is the total concentration of all oxidants present in a sample, reflecting the current oxidative load (Erel 2005).

If the reduced reproductive effort of migrants, as a group, allows them to maintain a superior physiological state at the end of breeding, we expect migrants to exhibit greater size-corrected mass, as they should be able to maintain or even increase body mass during the breeding effort. Migrants should also exhibit higher hematocrit. As stress negatively impacts immune system function and increases the quantity of WBC in circulation, migrants should exhibit a lower leucocrit and WBC count, and a lower heterophil to lymphocyte ratio. However, we cannot explicitly predict the effects of reduced reproductive effort on immunoglobulin levels, as the interpretation of immunoglobulin levels is still unclear (Morales *et al*. 2004). Finally, we expect migrants in better physiological state to exhibit higher triglyceride and lower glycerol levels, reflecting a maintenance or gain of fat stores, and lower oxidative stress (higher antioxidant capacity and lower oxidant levels).

Adult dippers were captured in mist-nets during the last week of the nestling phase of their final breeding attempt, since adults are difficult to capture after the young have fledged. Individuals were sexed based on the presence or absence of a brood patch and aged as either a yearling (second year, SY) or older (after second year, ASY) using the shape of the primary coverts and the presence or absence of a moult limit amongst the secondary coverts (Pyle 1997). We weighed all birds to the nearest 0.5g and measured the length of their right tarsus (to 0.01mm) and the combined length of the head and bill (to 0.1mm). Tarsus and head-bill length were later combined into a single measure of structural size using a principal components analysis (PCA). Size corrected mass was then calculated as the unstandardized residual of a linear regression of mass on structural size. As males are structurally larger and heavier than females (Green *et al*. 2009), PCAs and size corrected mass were calculated separately for each sex. For females, PC1 (the combined measure of structural size) accounted for 65.6% of variation in structural size (n = 19), while for males PC1 accounted for 70.8% of variance (n = 25).

Blood samples (up to 200μl) were collected from the brachial vein using heparinized capillary tubes and stored over ice until centrifugation, which occurred in the field as soon as possible thereafter (range: 5 minutes to 7 hours later; average 1.3 hours; n = 63). A few drops of whole blood were used to make air-dried blood smears. The remaining blood was centrifuged in hematocrit tubes at 12000rpm for 5 minutes to separate the plasma and cells (M24 Microhematocrit centrifuge, LW Scientific, Lawrenceville, GA). Hematocrit was then determined by dividing the height of the packed red blood cells by the total height of the blood column (measured to 0.01mm with dial callipers). Leucocrit was determined by dividing the height of the packed white blood cells (“buffy layer”) by the total. A dissecting microscope at 16x magnification aided in measuring the while blood cell layer. When more than one tube was drawn, results were averaged to yield a final score for each individual (1 to 4 capillary tubes per bird). The within-individual coefficient of variation (CV) for hematocrit was 3.4%, and

16.3% for leucocrit. The separated plasma was then stored on ice until freezing at -20°C at the end of the day, and was later transferred to -80°C for longer-term storage.

The air-dried blood smears were used to determine total and differential WBC counts, and the ratio of heterophils to lymphocytes (H:L ratio). The H:L ratio was determined from a differential WBC count, which, along with the total WBC count, were performed by trained personnel at Central Laboratory Services for Veterinarians (Langley, British Columbia).

The sampled plasma was analysed for immunoglobulins, triglyceride and free glycerol levels, antioxidant capacity and oxidative status. Plasma immunoglobulin levels were assessed using an enzyme-linked immunosorbent assay (ELISA) that has been previously validated in six wild bird species, including four passerines (Martínez *et al.* 2003). The method is described in detail in Bourgeon *et al.* (2006). Plasma was diluted to 1/8000 in carbonate-bicarbonate buffer (0.1 M, pH 9.6), and samples from each bird were run in duplicate (100μl diluted plasma per replicate). The intra-assay CV was 1.5%. Circulating free glycerol and total glycerol (free glycerol + triglycerides) were determined sequentially using a colourimetric endpoint assay. Absorbance was read 10 minutes after the addition of each reagent at 450nm in a microplate spectrophotometer (5μl plasma, 240μl regent A, 60μl reagent B, Sigma-Aldrich, St. Louis, MO). Assays were run in duplicate (or triplicate, where possible) using 5μl of plasma per replicate. Intra-assay CVs were 5.1% and 5.4% for determinations of free and total glycerol, respectively, and inter-assay CVs were 10.5% and 2.7%, respectively. Triglyceride concentrations were calculated as the difference between total and free glycerol concentrations. Total antioxidant capacity (TAC) and total oxidative status (TOS) were assessed using colourimetric methods developed by Erel (2004, 2005). The TOS methodology was modified by S. Bourgeon for smaller sample sizes (reduced to 10 μl of plasma per replicate from 35 μl). All samples were run in duplicate, and the intra-assay CVs were 1.7% for TAC and 4.5% for TOS. The results for TAC are expressed in mmol Trolox (a soluble analogue of vitamin E, an antioxidant) equivalent/L, and the concentration of oxidants is presented in μmol hydrogen peroxide equivalent/L. Sample sizes vary as immunoglobulin levels, TAC, and TOS were only assessed for birds breeding in 2007, and small plasma sample volumes occasionally prevented all measures being determined for all individuals. All triglyceride and glycerol assays were performed by I. Whitehorne, and all immunoglobulin, TAC and TOS assays were performed by S. Bourgeon. All plasma assays were conducted at Simon Fraser University.

Statistical methods

General linear models were used to test if previously observed differences in reproductive success and timing of breeding between migratory and sedentary (resident) individuals (Gillis *et al.* 2008) held true during the years of this study, while controlling for effects of year, male age, and female age. We then used Pearson's chi-squared tests and binary logistic regression to determine if within-breeding season survival and annual return rates differed between migrants and residents, while controlling for possible age, sex, and year effects.

We used both a univariate and multivariate approach to investigate if migrant and resident individuals differed in their physiological state late in the breeding season. We used general linear models to examine the effect of migratory strategy on each of ten physiological measures. We initially fit a full model including the main effect (migratory strategy) and all possible confounds that could influence these physiological measures (listed in Table 3.1). We sequentially removed all nonsignificant potential confounds (defined conservatively as $p > 0.1$) before evaluating the main effect of strategy. We subsequently used a subset of these physiological measures in a discriminant function analysis to determine if migrants and residents could be distinguished on the basis of their end-of-breeding physiological state (immunoglobulin levels, TAC and TOS were omitted from this analysis as they were only measured in one year).

We then used general linear models to assess whether the short-term physical workload or the longer-term reproductive workload influenced each of the ten physiological measures in migratory or sedentary individuals. We initially fit a full model containing the main effect (distance flown to provision young or total number of young raised during the season), an interaction term between migratory strategy and the main effect, and all possible confounds (Table 3.1). We sequentially removed all nonsignificant potential confounds ($p > 0.1$) before evaluating the interaction term. If nonsignificant, the interaction term was then dropped and the significance of the main effect evaluated. In all analyses we considered all datapoints to be independent since repeat sampling of the same individual in both years was rare ($n = 1$). All analyses were run in either GenStat v10 (VSN International Ltd, 2007) or SPSS v 16.0 (SPSS Inc, 2007).

Results

Breeding performance

Migrant pairs began incubation, on average, 11 days after residents (Julian date of incubation start, where Jan 1st = 1; migrants, 110 ± 3.0, n = 11; residents: 99 ± 1.7, n = 35; t = -3.29, p = 0.002, controlling for year). Pairs also initiated clutches earlier in 2006 than 2007 (2006: 96 ± 2.3, n = 23; 2007: 113 ± 2.1, n = 23; t = -6.05, p < 0.001, controlling for strategy), but neither male nor female age affected the timing of breeding (female age: t = 0.006, p = 0.99, n = 37; male age: t = 0.19, p = 0.85, n = 41; controlling for strategy and year). Despite breeding later, migrant pairs did not fledge significantly fewer young than resident pairs (migrants: 1.8 ± 0.5 young, n = 14; residents: 2.8 ± 0.3 young, n = 39; t = -1.59, p = 0.117), although the observed trend is consistent with significant differences detected in this population using a much larger dataset (Gillis *et al.* 2008). Number of young fledged also did not differ significantly between years (t = 0.57, p = 0.58, n = 53) or vary with the age of either parent (female age: t = -0.78, p = 0.44, n = 39; male age: t = 0.36, p = 0.72, n = 44). Sample sizes vary as incubation start dates were not known for all pairs, not all breeding individuals were aged, and not all nesting attempts successfully fledged young.

Survival

Most individuals that initiated a clutch survived their breeding attempt, and consequently the breeding season survival of residents was not significantly different from that of migrants (residents: 91% survived, n = 69, migrants: 92 % survived, n = 26, $\chi^2 = 0.25$, p = 0.88). The return rate from one breeding season to the next also did not differ significantly between residents and migrants (residents: 47% returned, n = 62, migrants: 56% returned, n = 16) when examined alone (χ^2 = 0.46, p = 0.50) or after controlling for potential effects of age, sex, and year (migratory strategy: χ^2= 0.008, p = 0.93; age: χ^2= 0.15, p = 0.70; sex: χ^2= 0.36, p = 0.55; year: χ^2= 3.20, p = 0.07; n = 75). However, the observed trend towards higher annual return rates in migrants is again in agreement with significant differences in survival detected using mark-recapture analysis of a larger dataset (Gillis *et al.* 2008).

Migratory strategy and physiological state

Migrants and residents did not differ in any of the ten measures of physiological state measured in this study (Figure 3.1, Table 3.2). A discriminant function analysis incorporating seven of the ten measures (size-corrected mass, hematocrit, leucocrit, WBC count, H:L ratio, triglycerides, and free glycerol) was also unable to distinguish between migrants and residents on the basis of overall physiological state (χ^2= 6.66 p = 0.47, n = 44). Only 55% of cases were correctly classified using a bootstrapping technique where each data point is sequentially omitted, the discriminant function re-calculated, and the omitted point classified using that function ("leave-one-out classification", SPSS v16.0). The discriminant function similarly failed to distinguish resident and migrant individuals when potential physiological covariates such as age, year, timing of breeding, body mass, time of day, and sampling lag were included (χ^2= 17.07, p = 0.20, n = 44, 64% of cases correctly classified).

Workload and physiological state

Neither the short-term physical workload (distance flown per hour to provision the young) nor the longer-term reproductive workload (total number of chicks reared) of an individual influenced any of the ten measures of physiological state measured in this study, after making Bonferroni corrections for multiple comparisons (Bonferroni corrected α of 0.05/10 = 0.005; Table 3.3). There was also no suggestion that the effects of short-term or long-term workload on physiology varied with the migratory strategy of an individual. If less conservative criteria are applied, our data suggest short-term workload is positively correlated with size-corrected mass and the number of young raised is positively associated with levels of free triglyceride (Table 3.3).

Discussion

We investigated if an apparent trade-off between reproduction and survival in migrant and resident American dipper is an expression of a physiologically-mediated cost of reproduction. We assessed if the differences in reproductive effort associated with these alternate life history strategies lead to differences in physiological state at the end of breeding that could potentially serve as a mechanistic link between survival and reproduction. We found no evidence that the reduced reproductive workload of migrants had any positive effect on their physiological state. In particular, we found no differences in either immune system function or oxidative stress, two physiological mechanisms that have been proposed to underlie the cost of reproduction. The lack of difference in physiological state with migratory strategy suggests that a physiologically-mediated cost of reproduction does not underlie the apparent trade-off between reproduction and survival between migrant and resident dippers.

We may not have detected physiological differences between migrants and residents at the end of the breeding season for several reasons. One possibility is that the years during which this study was conducted were atypical and the apparent trade-off between reproductive success and survival was not present. However, during this study we observed a trend for migrants individuals to fledge fewer young than residents, and migrants also tended to have higher annual return rates. Effect sizes were similar to those found by larger studies (migrants fledged on average 1.0 fewer young than residents, this study; vs. 1.4 fewer, Gillis *et al*. 2008), or were greater than expected (annual return rates 9% higher in migrants, this study; vs. 3.4% higher annual survival, Gillis *et al*. 2008), suggesting that the observed trends in reproduction and survival were nonsignificant due to sample size.

A second possibility is that significant differences in physiological state between the two strategies do exist, but our sample sizes were to small to detect them. However, this seems unlikely as the mean values for the physiological measures used are essentially identical between migrant and resident individuals, and we observed no consistent trends for visible but nonsignificant differences between the two groups. A multivariate approach also did not perform any better when attempting to distinguish between migrant and resident individuals on the basis of physiological state.

A third option is that the measures used are not influenced by reproduction or workload and have little to do with survival or overall health, and are inappropriate for the questions asked. However, these physiological measures have been widely used, even in studies of wild, free living populations, and many studies have found links between these measures and reproductive success and survival. For example, in both experimental and observational studies, size-corrected mass (Moreno *et al.* 1999), hematocrit (Hõrak *et al*. 1998), leucocrit (Moreno *et al.* 1998), total WBC count (Moreno *et al*. 2002), heterophil to lymphocyte ratio (Hõrak *et al.* 1998, Moreno *et al.* 1998, Ots and Hõrak

1996), immunoglobulin levels (Apanius and Nisbet 2006, Gustafsson *et al*. 1994) and antioxidant defences (Alonso-Alvarez *et al*. 2004) have been observed to vary with reproductive success. In addition, although studies linking such physiological variables to survival are few and tend to focus on juvenile birds, size-corrected mass (Lindén *et al*. 1992), white blood cell count and H:L ratios (Hylton *et al*. 2006), and immunoglobulin levels (Christe *et al*. 2001, Gonzalez *et al*. 1999) have been linked to survival. Single physiological measures such as these can be affected by a broad diversity of factors (see Table 3.1 for examples), and the utility of some physiological measures have been questioned due to an incomplete understanding of their ecological meaning (e.g. Adamo, 2004, Dawson and Bortolotti 1997). However, using a broad suite of such measures, such as we have, can provide a much fuller and more reliable picture of physiological condition than a single measure. Such broad suites of multiple physiological measures have been successfully used to distinguish urban and rural populations (Ruiz *et al*. 2002), track energetics and immune system function throughout the annual cycle (Owen and Moore 2006), assess habitat quality (Guglielmo *et al*. 2005, Owen *et al*. 2005), and effects of predation pressure and food limitation (Clinchy *et al*. 2004).

A final possibility is that there is no difference in physiological state between migrant and resident individuals at the end of breeding, and that natural variation between these groups in reproductive workload does not lead to differences in physiological state at the end of breeding. We believe this to be the case in this study. As the reduced reproductive success of migrant individuals, as a group, does not appear to result in enhanced physiological state, it is thus unlikely to be a direct cause of their generally higher survival. While migrant and resident dippers do not differ in physiological state at the end of breeding, this does not mean that the two groups are in the same physiological state at the start of breeding, which was not measured in this study. Migrants may have been in poorer condition at the beginning of or prior to the breeding season, limiting their ability to gain any physiological benefit from lower reproductive effort.

As the reduced reproductive effort of migrant dippers does not lead to better physiological state at the end of breeding (which could in turn affect survival), the source of the differential mortality between migrant and resident dippers remains unidentified. However, migrant and resident individuals differ in other ways that could affect survival independently of reproductive success. For example, resident individuals remain on and guard their multipurpose territories year round, while migrants maintain separate breeding and wintering areas (Morrissey 2004). The year-round maintenance and defence of a high-quality territory may impose a survival cost on resident dippers. Further study into the differences in behaviour and ecology between migrant and resident individuals is required to address the source of the mortality difference between the two life histories.

Table 3.1: Potential confounds controlled for in all stepwise univariate analyses of physiological measures.

Confounds were measured as follows: Age: yearling vs. older; Date: Julian date of start of incubation of the 1st clutch, where Jan 1 = 1; Time of day: hours past sunrise; Mass: total body mass in grams; Sampling lag: time elapsed between the bird striking the net and the blood sample being drawn, in minutes.

Physiological measure	**Potential confounds**	**References**
Size-corrected mass	Age Date Sex Time of day	Guglielmo *et al*. 2005 Moreno *et al*. 2002 Ormerod and Tyler 1990
Hematocrit	Date Sex Time of day	Dawson and Bortolotti 1997 Moreno *et al*. 2002 Owen *et al*. 2005
Leucocrit	Date Sex	Gustafsson *et al*. 1994 Moreno *et al*. 1998
Total white blood cell count	Sex	Moreno *et al*. 2002 Owen *et al*. 2005
Heterophil to lymphocyte ratio	Date Mass	Gustafsson *et al*. 1994 Ruiz *et al*. 2002
Immunoglobulins	Date	Gustafsson *et al*. 1994
Triglycerides	Mass Sampling lag Sex Time of day	Guglielmo *et al*. 2002 Owen *et al*. 2005 Williams *et al*. 1999b
Free glycerol	Mass Sampling lag	Guglielmo *et al*. 2002
Total antioxidant capacity	Age Mass	Costantini *et al*. 2008
Total oxidative status	Age	Costantini *et al*. 2008

Table 3.2: Predicted and observed effects of migratory status on the physiological state of American dippers at the end of the breeding season. General linear models were used to assess differences associated with migratory strategy in each of ten physiological measures, relating to four different aspects of health. Predictions from theory are given (see text for details), as well as average values for migrant and resident individuals. See Figure 3.1 for units. Potential confounds were controlled for and retained in the final model if $p < 0.1$. Asterisks indicate statistical significance of confounds ($^{*}p < 0.1$, $^{**}p < 0.05$, $^{***}p < 0.01$).

			Resident		**Migrant**				
	Variable	**Prediction**	**Mean ± s.e.**	**n**	**Mean ± s.e**	**n**	**t**	**p**	**Controlling for:**
General	Size-corrected mass	R < M	-0.1 ± 0.4	32	0.2 ± 0.6	12	-0.28	0.78	-
	Hematocrit	R < M	50.6 ± 0.5%	32	51.4 ± 0.9%	12	-0.78	0.44	Sex***, Year***, Sampling Lag**
Immune System	Leucocrit	R > M	0.4 ± 0.03%	32	0.4 ± 0.04%	12	0.35	0.73	-
	WBC count[†]	R > M	2.6 ± 0.2	32	2.1 ± 0.4	12	1.31	0.20	Year***
	H:L ratio[†]	R > M	1.2 ± 0.2	31	1.3 ± 0.2	11	-0.59	0.56	Sex*, Year**, Mass**
	Immunoglobulins	n/a	0.30 ± 0.02	15	0.31 ± 0.04	8	-0.10	0.92	Date**, Mass*
Lipid Metabolism	Triglycerides	R < M	1.2 ± 0.1	28	1.1 ± 0.2	10	0.51	0.61	-
	Free Glycerol	R > M	0.6 ± 0.0	27	0.5 ± 0.01	9	1.30	0.20	Age**, Sex**, Year*
Oxidative Stress	TAC	R < M	0.56 ± 0.02	16	0.60 ± 0.03	9	-1.09	0.29	Sex**
	TOS	R > M	0.72 ± 0.09	16	0.89 ± 0.11	9	1.23	0.23	-

[†] Measures determined at a commercial laboratory. A linear mixed model was first used to determine if results were affected by the identity of the technician processing the samples. Little variance was associated with the ID term for all cases ($p > 0.1$, χ^2) so the random identity term was dropped and analyses performed as general linear models.

Table 3.3: Observed relationships between individual short-term and long-term workload and ten measures of physiological state in American dippers. General linear models were used to assess relationships between short-term (distance flown per hour to provision the young) and long-term (total number of young fledged) workload and each of ten physiological measures. Observed direction of relationship is included in brackets where significant at $p < 0.05$. Potential confounds were controlled for and retained in the final model if $p < 0.1$. Asterisks indicate statistical significance of confounding factors ($^{*}p < 0.1$, $^{**}p < 0.05$, $^{***}p < 0.01$).

		Short-term workload						**Long-term workload**					
		Main effect of workload		**Workload by strategy interaction**				**Main effect of workload**		**Workload by strategy interaction**			
		t	**p**	**t**	**p**	**n**	**Controlling for**	**t**	**p**	**t**	**p**	**n**	**Controlling for**
General	Size-corrected mass	2.14	0.039 (+)	-0.55	0.59	39	-	0.37	0.72	1.75	0.09	42	-
	Hematocrit	0.91	0.37	-1.41	0.17	39	Sex***, Year***, Sampling Lag**	-1.83	0.08	0.12	0.90	43	Sex***, Year***, Sampling Lag**
Immune System	Leucocrit	1.97	0.06	0.53	0.60	39	-	-0.04	0.97	-1.59	0.12	43	-
	WBC count†	1.23	0.23	-0.50	0.62	39	Year***	0.14	0.89	-0.91	0.37	42	Year***
	H:L ratio†	0.95	0.35	-0.29	0.78	39	Mass***	0.84	0.41	-1.22	0.23	42	Sex*, Date**, Mass***
	Immunoglobulins	-0.12	0.90	-1.34	0.20	22	Sex***, Date***	-2.00	0.06	0.89	0.40	23	Sex***, Date***
Lipid Metabolism	Triglyceride	1.39	0.17	0.76	0.46	33	Year***, Time***	2.21	0.034 (+)	1.20	0.24	37	Mass*
	Free Glycerol	0.81	0.42	0.38	0.71	33	Year***, Mass**	-0.58	0.57	0.64	0.53	34	Age**, Date**, Mass**
Oxidative Stress	TAC	0.21	0.84	0.48	0.64	23	Sex**	-1.46	0.16	-1.74	0.10	24	Sex**
	TOS	0.38	0.71	1.68	0.11	23	-	0.27	0.79	-0.76	0.46	24	-

†Measures determined at a commercial laboratory. See Table 3.2 for details of analysis.

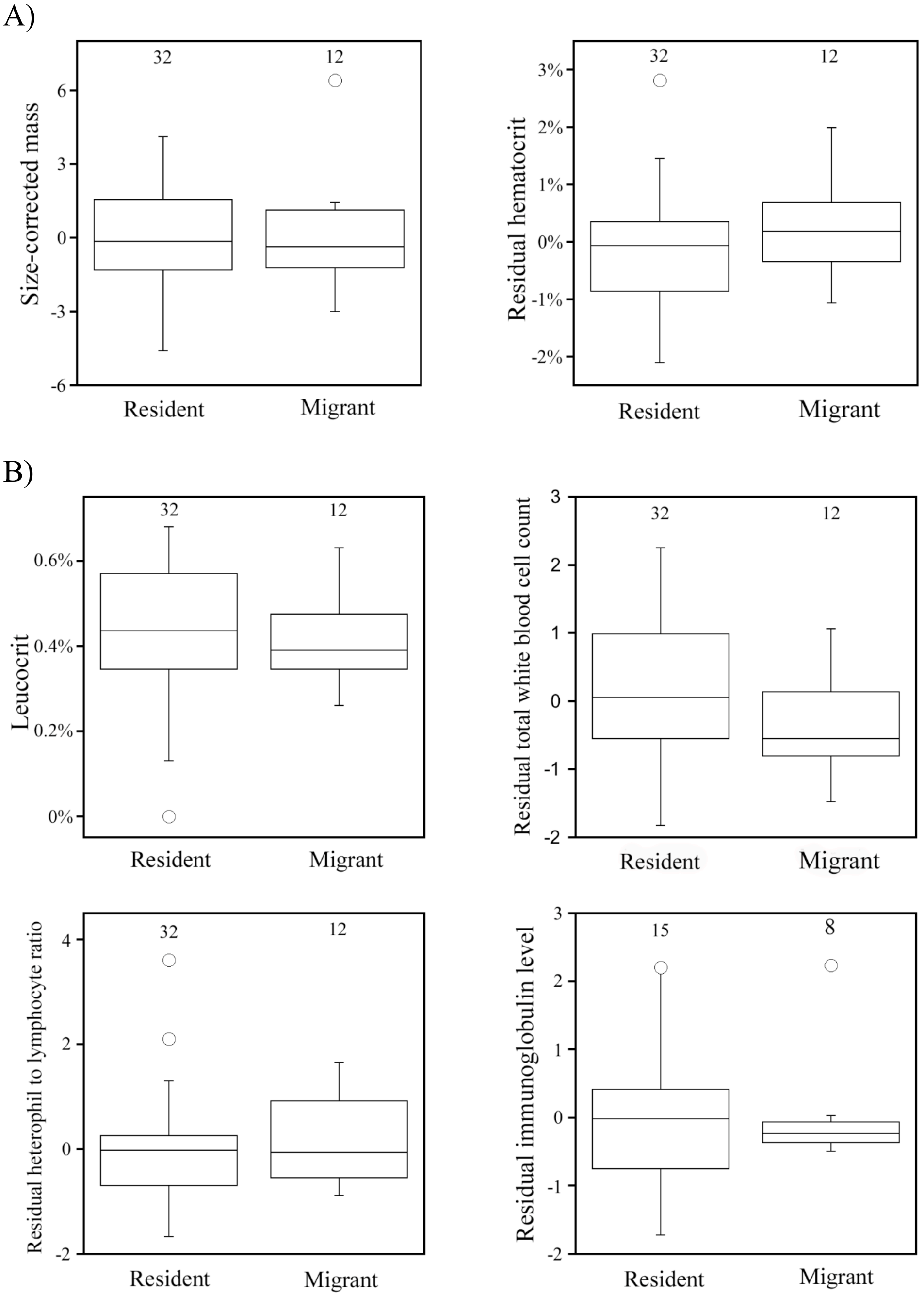

Figure 3.1: End-of-breeding physiology of migrant versus resident American dippers. Values for each individual are corrected for significant confounds (see Table 3.2). Boxplots indicate median, 1st and 3rd quartiles, minimum and maximum values (and outliers). None of the ten physiological variables measured vary significantly with strategy at $p < 0.05$. See Table 3.2 for p-values, and Methods for the details of measurement. A) General condition measures: *Size corrected mass* is expressed in grams. See Methods for details of calculation. *Hematocrit*, the volume of blood consisting of red blood cells, is expressed as % of volume. B) Immune System: *Leucocrit*, the volume of blood consisting of white blood cells, is expressed as % volume. The *total white blood cell count* is expressed as thousands per μl of blood. The *ratio of heterophils to lymphocytes* is unitless. *Immunoglobulin* levels are presented in arbitrary absorbance units.

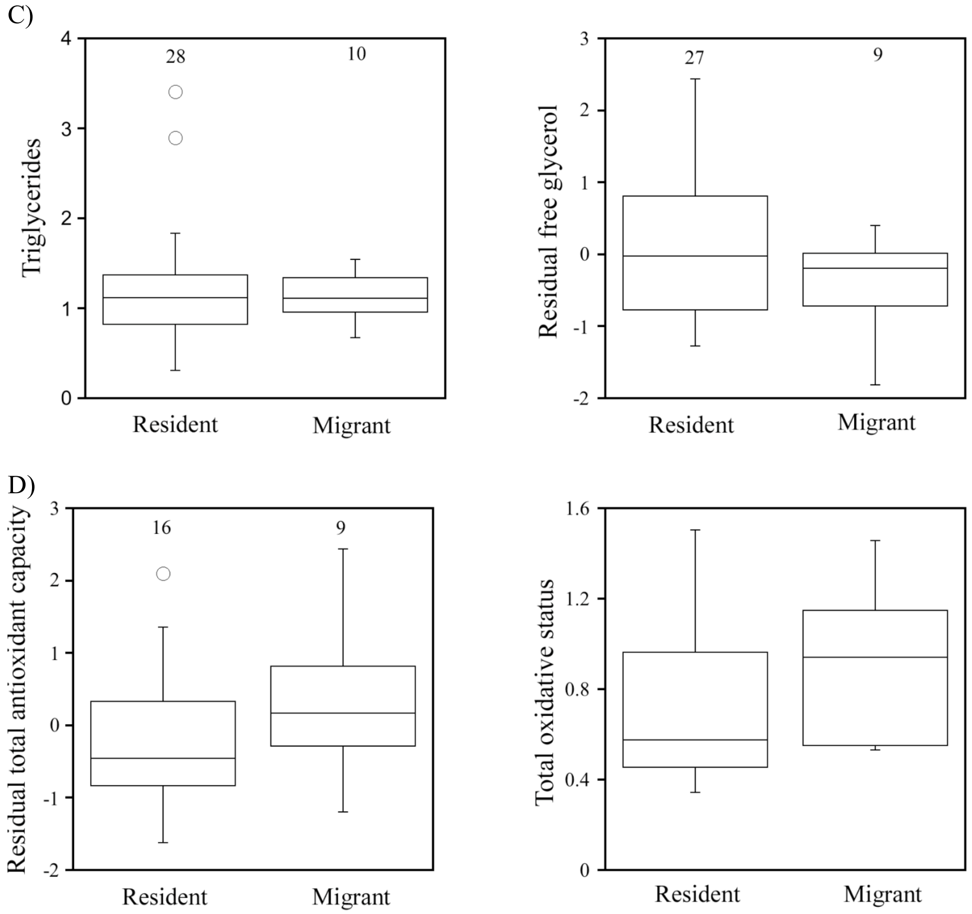

Figure 3.1 (continued): End-of-breeding physiology of migrant versus resident American dippers. C) Lipid metabolism: Both *triglycerides* and *free glycerol* levels are expressed as concentrations (mmol/L). D) Oxidative Stress: *Antioxidant capacity* is expressed in mmol/L Trolox equivalent; *oxidative status* is expressed as mmol/L hydrogen peroxide (H_2O_2) equivalent.

CHAPTER 4: WINTERING ECOLOGY OF MIGRATORY AND SEDENTARY AMERICAN DIPPERS, *CINCLUS MEXICANUS*

Abstract

Winter is a critical period for songbirds that overwinter in temperate areas, as they must endure cold temperatures, reduced food availability and shorter daylight that reduces foraging time and lengthens the nightly fast. American dippers are aquatic passerines noted for their ability to endure harsh conditions, but despite adaptations to their aquatic lifestyle, winter conditions can still influence survival and population growth rates. Our study population in the Chilliwack River of southwestern British Columbia, Canada, consists of altitudinal migrants and sedentary (resident) individuals. Despite individuals of the two strategies overwintering in the same area, residents have a higher annual mortality rate. From September 2006 to March 2007, we investigated if staying on a multi-purpose territory year round, as residents do, was associated with differences in foraging behaviour, energetic intake, or physiological state that could potentially explain the higher mortality of resident individuals. Physiological state was assessed using a broad suite of measures that relate to general condition, immune system function, lipid metabolism, and oxidative stress. We also assessed if migrant and resident individuals differ in site fidelity. We found that residents spent less time foraging and used shallow-water foraging methods more often than migrants. However, this did not lead to any differences in energetic intake or physiological state between the two groups, indicating that the observed differences in foraging probably do not underlie the different

mortality rates. Both migrants and residents tended to increase their rate of energetic intake as the winter progressed, which corresponded with an increase in both size-corrected mass and triglyceride levels, indicating a build-up of fat reserves as the winter advanced. We also found that migrants show reduced site fidelity, and may therefore benefit from greater spatial flexibility. As a result, migrants may have a greater ability to respond to changing conditions such as floods, while residents may be constrained to remain near and defend their nesting site. The difference in site fidelity between migrants and residents does not lead to differences in physiological state, but may affect the probability of relatively rapid-death events such as starvation during floods.

Introduction

Winter is a critical period for bird species that remain in temperate regions year-round. They must endure cold temperatures, reduced food supplies, and shorter daylight that reduces foraging time and lengthens the nightly fast. Adaptations to survive these harsh conditions include changes in both physiology and behaviour, such as the building up of fat reserves (e.g. Evans 1969, Gosler 2002), food-caching (Brodin 2005), winter flocking to improve food intake (Beauchamp 1998, Hogstad 2003), and changes in habitat use to minimize thermoregulatory costs (Huertas and Diaz 2001, Jenni 1991). Despite such adaptations, winter conditions are challenging for small species, with cold temperatures, reduced food and severe weather all increasing mortality risk (Newton 1998).

Harsh winter conditions may pose a particular challenge for species that forage in water. The greater thermal conductance of water means heat is lost much faster in water than air and the compression of feathers by water further reduces the insulating quality of plumage, so birds foraging in water must increase metabolism to stay warm (Kooyman *et al*. 1976, Stahel and Nicol 1982). Heat loss is more pronounced for smaller species (de Vries and van Eerden 1995), such as Dippers (*Cinclus* spp.). Dippers are nevertheless noted for their ability to persist in harsh conditions. For example, dippers have been reported to endure extremely cold temperatures (-57˚ C in northern Alaska, Gabrielson and Lincoln 1959; -40˚ C in Montana, Bakus 1959a), overwinter in very northerly habitats (64˚ N in Sweden, Lundberg *et al*. 1981; 58˚ N in Alaska, Willson and Hocker 2008), and cluster around ice holes and other open areas as rivers freeze (Bakus 1959b, Whitney and Whitney 1972). A key adaptation that allows dippers to forage in these conditions is their thick, waterproof plumage. Dippers have denser plumage than other passerines and a thick down layer, which greatly reduces heat loss and allows dippers to maintain normal body temperature when ambient temperature is as low as -30˚ C (Kingery 1990). However, winter is known to be the period of greatest energy stress (D'Amico and Hémery 2007), and winter conditions have been shown to influence survival and population growth rates of both American (*Cinclus mexicanus*) and white-throated dipper (*Cinclus cinclus*) (Loison *et al*. 2002, Price and Bock 1983, Sæther *et al.* 2000, Willson and Hocker 2008).

Long-term monitoring of a population of American dipper in southwestern British Columbia, Canada, has revealed that the majority of individuals are altitudinal migrants, while some individuals remain at low elevation year-round (Morrissey *et al*. 2004). Individuals appear to retain their migratory strategy for life, as switching is rare (Gillis *et al*. 2008). Migrants produce fewer fledglings each year than sedentary individuals (residents) because they begin breeding later and consequently they are less likely to initiate a second brood. However, the lower productivity of the migrants is partially offset because they have a higher annual survival than residents (Gillis *et al.* 2008).

As winter is harsh and presumably a period of high mortality, we investigate if the differences in annual survival rates between migrant and resident American dipper could result from differences in their wintering ecology and/or behaviour. We used focal observations to determine if the use of multipurpose year-round territories requires residents to expend greater effort foraging or reduces energetic intake rates compared to migrants, which are not constrained to remain near and defend their nesting site. We then investigated if differences in foraging behaviour or costs associated with maintaining a year-round territory lead to residents being in poorer physiological state than migrants. Finally, we assessed if migrants are less constrained to remain at one location through the winter, which may increase their ability to deal with changing conditions during events such as floods.

Methods

Study species and study site

American dippers (hereafter dippers) are small obligate aquatic passerines that inhabit steep mountain streams and rivers in western North America, ranging from Alaska to Mexico (Kingery 1990). Their winter range is limited only by presence of open, flowing water (Kingery 1990), and populations in mountainous areas are often partially migratory (e.g. Bakus 1959b, King *et al*. 1973, Morrissey *et al*. 2004, Willson and Hocker 2008). We have studied a marked population of migratory and sedentary (resident) dippers in the Chilliwack River watershed, located approximately 100km east of Vancouver, British Columbia, Canada, since 1999 (Morrissey 2004). Residents defend linear stretches of the main stem of the Chilliwack River (300m—1km in length) as breeding territories and remain on these territories year-round. Migrants establish breeding territories at higher elevation on tributaries, but overwinter at lower elevation with the residents (Gillis et al 2008).

We monitored ten study sites used by wintering dippers from September 2006 to March 2007. Study sites on the Chilliwack River and the lowest reaches of its tributaries were approximately 0.8 km long (range 0.6 to 1.3), and separated by 3.1 km (range 0.3 to 14.3). These sites have been censused regularly throughout winter (November to March) and the majority of accessible stretches of the Chilliwack River and its major tributaries have been monitored during the breeding season (late March to June) every year from 1999 onwards.

General methods

We captured dippers using mist nets set up across shallow stretches of the river and its tributaries throughout the year. All individuals captured were marked with a numbered metal band and a unique combination of three colour bands. Since 2006, all birds have been aged upon first capture as either juvenile (hatch year HY, or second year SY) or adult (after hatch year AHY, or after second year ASY), based on shape of the primary coverts and presence or absence of a moult limit among the secondary coverts (Pyle 1997). Individuals were sexed on the basis of behaviour (only females incubate and brood, Kingery 1996) and morphology (in this population males are on average 16% heavier and morphological measures are 2-9% larger; Green *et al*. 2009). However, there is some size overlap between the sexes, so the sex of some individuals captured outside the breeding season could not be determined.

The migratory strategy of adult individuals was determined based on resighting history. Individuals were classed as resident if they bred on or within 1 km of the main stem of the Chilliwack River and remained at that site throughout fall and winter. Individuals were classed as migrant if they were seen in the same area for two or more winters but had not bred there. Adults first banded during the fall and winter of 2006/2007 were classed as migrant if they consistently inhabited the same area throughout winter and survived the winter (were seen in January or later), but disappeared before the breeding season. Birds of unknown age and juveniles (which have not yet established a migratory strategy) were excluded from all analyses.

Time budgets and foraging behaviour

Focal observations were conducted on 19 adult dippers (9 migrants, 10 residents) between 21 September and 23 November 2006. Each individual was observed for one session, lasting approximately one hour (56 ± 5 minutes). We obtained time budgets by recording the instantaneous activity of the bird every 60 seconds, which was classified into 3 major categories and 10 subcategories (Table 4.1).

The energetic intake of the focal individual was determined by simultaneously recording the number, type, and size of all food items consumed. We estimated the energy intake of each individual observed by multiplying the number of each prey type consumed per hour of observation by the average mass and energy content per unit mass of that prey type (Table 4.2). Invertebrate prey items were classed as small, medium or large by comparing their length to the length of the bird's bill (small, < ¼; medium, ¼ to ½; large, > ½ bill length; bill length = 22mm, Donnelly and Sullivan 1998). To determine the average mass of an invertebrate prey item of each size class, benthic invertebrates were collected by kick-sampling, preserved in ethanol, and sorted into each size class. Fifty individuals of each size class were dried for 24h at 40 °C and weighed to the nearest μg to produce an average dry weight (DW) for each size class. Mass of salmon eggs was estimated using published values for local populations (Fleming and Gross 1990). We used photos (n = 11) to determine the average length of fish consumed by comparing the size of the fish to the length of the bill. We then used a published length-weight relationship for juvenile sockeye salmon (Chingbu 2001) to determine average mass. Energy content values for all prey types were drawn from the literature (Table 4.2).

Physiology

We used a broad suite of measures to examine whether the migratory strategy of an individual influenced their physiological state during the fall and winter. Ten measures relating to four different aspects of health were assessed: general condition measures (size-corrected mass and hematocrit), immune system function (leucocrit, total white blood cell count, the ratio of heterophils to lymphocytes, and immunoglobulin levels in peripheral blood), metabolism of lipid stores (levels of circulating triglycerides and free glycerol), and oxidative stress (total antioxidant capacity and total oxidative status of blood plasma). See Chapter Three (p 41) for some context of these measures.

We captured a total of 88 individuals (28 female, 41 male, 19 unknown) at the 10 study sites between mid-September 2006 and January 2007. This sample included 11 known residents and 24 known migrants, with the remainder being juveniles, of unknown age, or adults whose migratory strategy could not be determined. Individuals were weighed to the nearest 0.5g and measured (combined head-bill length to 0.1mm, and length of the right tarsus to 0.01mm). Tarsus and head-bill length were combined into a single measure of structural size using a principal components analysis (PCA), and size-corrected mass was then calculated as the unstandardized residual of a linear regression of mass on structural size. As males are structurally larger and heavier than females, PCAs and size corrected mass were calculated separately for each sex. For known-strategy adult females, PC1 (the combined measure of structural size) explained 83.4% of variation in size (n = 9); while for known-strategy adult males, PC1 explained 64.3% of variation in size in known-strategy males (n = 20). Size-corrected mass could not be calculated for 6 migrants as their sex could not be determined.

We collected a blood sample from all adults captured by puncturing the brachial vein and collecting the blood in heparinized capillary tubes. Blood was stored over ice until centrifugation, which occurred in the field, as soon as possible after collection (3 ± 1.3 hours, range 25 minutes to 5 hours). A few drops of blood were used to make an air-dried blood smears for later analysis of total and differential white blood cell counts, which were performed by trained personnel at Central Laboratory Services for Veterinarians (Langley, British Columbia). The remaining blood was centrifuged in hematocrit tubes at 12 000 rpm for 5 minutes to separate the plasma and blood solids (M24 Microhematocrit centrifuge, LW Scientific, Lawrenceville, GA). Hematocrit (packed blood cell volume) and leucocrit (packed white blood cell volume, the “buffy layer”) were then determined by measuring the height of the separated column (red blood cells and white blood cells respectively) and diving by the total height of all packed cells plus plasma. The plasma was then separated and stored on ice until freezing at -20°C at the end of the day, and was later transferred to -80°C for longer-term storage. The sampled plasma was later analysed for levels of immunoglobulins, free glycerol and triglycerides, antioxidant capacity and oxidative status. Details of the assay methodologies can be found in Chapter Three (p45). All assays were performed at Simon Fraser University.

Movement and site fidelity

We conducted weekly censuses of the 10 study sites from September 2006 to December 2006, and bi-weekly censuses from January 2007 to March 2007. During each census, an observer walked the riverbank of each site, identifying all banded dippers present within site boundaries. Colour bands were read with the aid of 8x binoculars or a 20-60x spotting scope.

We used this census data to calculate the site fidelity of all colour-banded residents and migrants at the 10 study sites. To avoid confounding mortality with site fidelity, we used only individuals that were known to have survived the winter (i.e. seen in January or later, n = 15 migrants, n = 9 residents). Site fidelity was calculated as the proportion of censuses when the bird was observed at its wintering site, from the first census it was observed until the end of January (proportions were based on 4 to 13 censuses). Census data from February and March was not used when calculating site fidelity of individuals because migrants may begin to move towards breeding grounds in these months (Morrissey *et al*. 2004).

Statistical methods

We used general linear models to examine if the migratory strategy of an individual influenced their foraging behaviour (proportion of time spent foraging and frequency of use of different foraging methods) or rate of energetic intake. We initially fit a full model including strategy, a strategy by date interaction, and date (measured as days past September 1st). A final model was selected by sequentially removing nonsignificant terms, starting with the interaction term, until only significant terms ($p \leq 0.05$) remained. As data were collected over 9 weeks from September to November, during presumably progressively worsening conditions for the birds (e.g. decreasing day length and lower temperatures), we tested only linear date effects in the models.

We also used general linear models to examine whether an individual's migratory strategy affected any of the ten measures of physiological state. We initially fit a full model containing migratory strategy, date, and a strategy by date interaction term, as well as several potential confounds (sex, body mass, time since sunrise, and the time lag between capture and drawing the blood sample) that have been shown to affect some of the physiological measures used (see Chapter Three, Table 3.1). We sequentially removed all nonsignificant potential confounds ($p > 0.05$). We then evaluated terms of interest (strategy, date, and a strategy by date interaction term), again sequentially removing nonsignificant terms, leaving only significant effects in the final model. Sample sizes vary as not all data was available for all individuals. To maintain maximum sample size, models were rerun with any additional data that could be added after terms with missing values were dropped.

Finally, we used a form of logistic regression to examine if site fidelity differed with migratory strategy. To avoid problems associated with proportion data calculated from varying sample sizes, we used the “modelling of binomial proportions” function in GenStat (v10, VSN International Ltd, 2007), which weights each data point by sample size (i.e. the number of censuses from the first sighting of that individual until the end of January). All data presented are means ± 1 standard deviation.

Results

Foraging behaviour and energetic intake

Residents spent significantly less time foraging than migrants (residents 58 ± 12% of the time, n = 10; migrants 69 ± 8%, n = 9; t = 2.25, p = 0.04; Figure 4.1a). The proportion of time residents and migrants spent foraging did not change over the course of the winter (date, expressed as days past Sept 1st; t = -0.80, p = 0.44), and the two groups did not respond differently to date (strategy by date interaction: t = 0.04, p = 0.97; n = 19 for all).

In addition, residents used shallow-water methods of foraging (See Table 4.1 for definitions) significantly more often than migrants (residents 38 ± 20% of time foraging, n = 10; migrants 21 ± 10%, n = 9; t = 2.19, p = 0.04; Figure 4.1b). This pattern was also consistent over the course of the winter and did not change with date (date: t = -0.66, p =0.52), and effects of date did not vary between migrants and residents (strategy by date interaction: t = -0.33, p = 0.75; n = 19 for all).

Despite spending different amounts of time foraging and using different methods, migrants and residents did not differ in energetic intake (migrants 19.3 ± 8.7 kJ/hr, n = 8;

resident 16.3 ± 9.1 kJ/hr, $n = 10$; $t = -0.68$, $p = 0.50$; controlling for date, Figure 4.1c). However, there was an increase in energetic intake with date ($t = 2.06$, $p = 0.06$, Figure 4.2a). This increase with date did not vary by strategy (strategy by date interaction: $t = 1.11$, $p = 0.28$; $n = 18$ for all). One outlier was removed from analysis of energetic intake; the bird was observed foraging in an outlet drain from a fish hatchery while incoming salmon were being processed for eggs. The bird consumed 46 salmon eggs in the space of one hour, and consequently had an energetic intake at least twice that of any other individual observed.

Physiology

Migrants and residents did not differ in physiological state during winter. None of the 10 physiological measures differed significantly between migrant and resident individuals (Table 4.3), after controlling for potential confounds (the time lag between capture and taking the blood sample, body mass, sex, and the time of day). There was, however, some seasonal variation in 2 of the 10 measures. Size-corrected mass increased with date ($t = 2.13$, $p = 0.04$, $n = 28$, Figure 4.2b), as did triglyceride levels ($t = 3.04$, $p < 0.01$, $n = 27$, Figure 4.2c). Neither of these date effects varied with strategy (strategy by date interaction, $p > 0.1$ for both). In some cases, missing values for potential confounds were replaced with the mean value to maintain the maximum sample size; however results were the same if the individuals with missing data were excluded.

Site fidelity

We observed average of 42 ± 13 individuals per census, of which about 40% were marked. Wintering migrants were observed at all 10 study sites, while residents were found at 6 of the 10 sites. Both migrants and residents appear to mostly remain within a particular "home range" throughout winter, as the large majority of individuals (81 of 87 banded birds observed) were observed at only 1 of 10 sites throughout the winter. The four migrants that were seen at a second site travelled 0.6, 3.3, 4.3 and 6.9 km between sightings. Only two residents were ever seen at a second site, having travelled 1.0 and 2.1 km from their respective nest sites.

Migrant individuals exhibited significantly lower site fidelity (proportion of censuses when the individual was observed on its wintering site, from first sighting to the end of January) than residents ($t = 3.32$, $p < 0.001$, $n = 24$; Figure 4.3). Resident individuals were observed on their wintering site during 70 ± 16% of censuses ($n = 9$), while migrants were observed only 53 ± 24% of the time ($n =15$).

Discussion

Dippers are known to endure particularly harsh and challenging conditions during winter. Despite their adaptations to cold temperatures and aquatic lifestyle, winter may still be a period of high mortality. In our partially migratory population of American dipper, resident (sedentary) individuals have lower annual survival rates, and we investigated if remaining on and defending a multi-purpose territory year-round imposes costs on resident individuals that may underlie their higher mortality.

Despite some differences in foraging behaviour, we found no evidence that residents were in poorer physiological state during winter. Residents spent less time foraging and used shallow-water foraging methods more often, but surprisingly, these differences did not lead to differences in energetic intake between the two groups.

However, due to small sample size and indirect determination of energetic intake (which may introduce substantial error), our power to detect significant differences is relatively low. In addition, we only assessed energetic intake early in the season. During a later period (i.e. December to February) conditions for the dippers may be more challenging and the observed differences in foraging behaviour (which did not change as the season progressed) may have a more pronounced effect on energetic intake.

We did not find any evidence that migratory strategy correlated with an individual's physiological state, despite the differences in foraging behaviour and site fidelity (see below). There was also no difference in how migrants and residents responded to the advancing winter. The only changes that occurred over time were the increase in size corrected mass and an increase in triglyceride levels, and the rate of these changes did not differ between migrants and residents. There is therefore little to suggest that remaining in an all-purpose territory constrains residents to forage in areas that require them to expend more effort foraging or reduce energetic intake, nor does it appear to impact their day to day physiological state. The lower survival of residents thus does not appear to be explained by differences in foraging behaviour and energetic intake.

The few physiological changes that we did observe as the winter progressed appeared adaptive, rather than a deterioration of physiological state. We saw no changes in our measures of oxidative stress or immune system parameters. We did, however, observe an increase in size corrected mass, which can indicate the building-up of fat reserves. This is supported by the significant increase in triglyceride in blood plasma with date, as triglyceride levels are an indicator of fat deposits and/or the rate of fat deposition (Guglielmo *et al.* 2002, 2005, Williams *et al.* 1999b). This agrees well with our observation that energetic intake of both migrants and residents increased with date. Together, these results indicate that as fall progressed into winter, dippers increased their energetic intake to build up fat reserves. Such fat reserves serve as a buffer against reduced food availability, lower temperatures, and shorter day lengths that reduce foraging time and lengthen the nightly fast (Gosler 2002). This is consistent with the observation that small birds generally manage their fat stores to balance starvation and predation risk, and tend to increase their fat stores as conditions become increasingly variable or unpredictable (Brodin 2007).

Movement patterns during winter may also influence survival rates, as widely ranging individuals may be able to better respond to variable food supply than sedentary individuals (Brown and Long 2007, Brown and Sherry 2008). Winter site tenacity is variable between populations of dippers, ranging from highly mobile throughout winter (e.g. Price and Bock 1983, Willson and Hocker 2008), to sedentary, with individuals moving only in the face of extreme events such as icing-over of their habitual stretch of river (e.g. Bakus 1959b). In this population, winter movement of adults is quite limited, as only a handful of individuals were observed on more than one study site over the course of the winter. This confirms earlier reports of limited winter movement in this population (Morrissey *et al* 2004). However, despite limited movement, we found that migrants exhibit reduced site fidelity (i.e. were present on a given study site less often) compared to residents, which is consistent with earlier findings that migrants have a reduced resighting probability (Gillis *et al.* 2008). While this apparent lower site fidelity of migrant individuals may be a result of lower detectability, we do not believe this to be the case. The majority of our census sites contain both residents and overwintering migrants, so any differences in visibility between the sites should not lead to an apparent difference in resighting probabilities of the two groups. Our focal observations also indicate that migrants and residents do not differ in the amount of time the spent at more visible activities (such as swimming, walking and flying; I. Whitehorne, unpublished data) which could affect detectability. Therefore, we believe the observed difference in site fidelity is due to a true difference in the amount of time individuals are present on site and not a result of differences in detectability.

This difference in site fidelity poses the question of why resident individuals exhibit greater site fidelity than migrants. Dippers can be nest-site limited (Loegring and Anthony 2006, Tyler and Ormerod 1994) and resident nest-sites, having a higher annual and lifetime productivity (Gillis *et al*. 2008), are presumably highly desirable for juvenile individuals who are seeking to establish their own territory. If residents are constrained to remain near their nest site and defend it, they should exhibit territorial defence behaviours throughout winter and do so more than migrants or juveniles. In this population, residents, migrants and juveniles will exhibit aggressive behaviour towards other birds during winter (I. Whitehorne, pers. obs). Similar behaviour has been observed in other populations (Bakus 1959b, Price and Bock 1983, Whitney and Whitney 1972), but the degree to which this is territory defence, defence of personal space, or establishment of a hierarchy is still unknown (Tyler and Ormerod 1994). Unfortunately we were unable to assess the relative intensity or frequency of these behaviours between residents, migrants, and juveniles in our population.

Our data suggests that migrants have somewhat larger home range sizes than residents. While individuals only rarely move between study sites during winter, migrants are less likely to be observed at a given study site, suggesting they are more likely to move outside the monitored census areas. It thus appears that migrants generally have home ranges that are larger than our study sites, but not large enough to encompass more than one site, while resident home ranges likely do not greatly exceed the size of the study sites. Dippers preferentially feed in certain restricted areas (American dipper, Thut 1970; brown dipper, Eguchi 1988, cited in Eguchi 1990), and shallow riffles appear particularly important (white-throated dipper, Tyler and Ormerod 1994). Even small changes in water level can shift the location of such prime feeding areas. The greater spatial flexibility (i.e. larger wintering home range) exhibited by migrants may allow them greater access to prime feeding areas as water levels change, which could enhance survival during periods of variable water flow such as floods.

In conclusion, we believe that migrant individuals may benefit from increased spatial flexibility in the face of changes in water level and food supply, while residents may be constrained to remain near and defend their nesting site. These differences do not result in improved physiological state for migrants, but may instead reduce the possibility of “sudden death” events. Due to small size and rapid metabolism, starvation, for example, takes place very quickly in small passerines and it is highly unlikely that a starving individual will be sampled in the brief interval between perfect health and death (Newton 1998). Use of radios to accurately map resident and migrant home range sizes and responses to water level changes would be informative. In addition, further work on the relationship between water-level variability and mortality rates is needed, as differences in migrant and resident mortality should be associated with periods of major flux in water levels.

Table 4.1: Behavioural categories used to construct time-budgets for wintering migrant and resident American dippers.

Major category	**Subcategory**	**Definition**
Foraging	Shallow	Pecking at substrate or holding/manipulating item in bill, while standing or wading
	Deep	Head-dunking (submerging head in deep water while swimming or standing on a midstream rock) or diving (body fully submerged, head under, feet not touching substrate)
	Aerial	Flying out in pursuit of airborne prey
Mobility	Fly	Powered flight, greater than 1m distance
	Walk	Walking with head up
	Wade	In water at least up to knee joint, walking
	Swim	In water at least up to belly, without legs touching substrate
Other	Vocalize	Song or alarm call
	Stand	No movement
	Preen	Using bill to preen or stretching/scratching

Table 4.2: Determining energetic content of prey items consumed by wintering American dippers.
Energy values for each item were calculated from the average mass and energy content per unit mass of that food type. Invertebrates were collected locally, dried and weighed; all other values are derived from the literature. Three kinds of values were taken from the literature: ^{A} energy content per unit mass, ^{B} mass, and ^{C} length-weight relationships. DW, dry weight; WW, wet weight.

Item Type	**Size**		**n**	**Mass**	**Energy Content**	**Energy per item**	**Sources**
	Bill length	**mm**					
Small Invertebrate	<1/4	< 6	50	0.59 mg DW	22.44 J/mg DW^{A}	13.2 J	^{A}Brey *et al.* 1988
Medium Invertebrate	1/4 to 1/2	6 to 10	50	4.04 mg DW		90.6 J	
Large Invertebrate	>1/2	> 10	50	25.5 mg DW		572 J	
Salmon Egg	-	-	-	166 mg WW^{B}	7.8 J/mg WW^{A}	1.3 kJ	^{A}Hendry and Berg 1999 ^{B}Average value from three locations within the Chilliwack River watershed, Flemming and Gross 1990
Fish	Average 2.0x	44	11	1.55 g WW^{C}	4.4 kJ/g WW^{A}	6.8 kJ	^{A}Boldt and Haldorson 2004, Dempson *et al.* 2004 ^{C}Calculated from length, Chingbu 2001

Table 4.3: Physiology of wintering migrant and resident American dippers.
Least-square means for migrant and resident individuals are shown, with other significant variables ($p \leq 0.05$) retained in the model listed. Direction of other significant effects (see text for list of potential confounds tested) are included in brackets as (+) positive or (–) negative correlations, or as > or < for categorical levels. Strategy by date interactions were also tested (all nonsignificant, $p > 0.05$). Sample sizes vary as not all data was available for all individuals. Asterisks indicate statistical significance (*$p < 0.1$, **$p < 0.05$, ***$p < 0.01$).

Response variable	**Migrant**	**n**	**Resident**	**n**	**t**	**p**	**Controlling for:**
Size-corrected mass	0.3 ± 0.5	17	-0.5 ± 0.7	11	-0.88	0.39	Date (+)*
Hematocrit	49.5 ± 0.6%	23	50.3 ± 0.9%	11	0.76	0.40	-
Leucocrit	0.5 ± 0.04%	22	0.6 ± 0.06%	11	1.51	0.14	-
White blood cell count†	4.0 ± 0.3	22	4.3 ± 0.5	9	1.86	0.59	Time (+)***
Heterophil to lymphocyte ratio†	1.3 ± 0.2	22	1.5 ± 0.2	9	0.74	0.47	-
Immunoglobulins	0.36 ± 0.01	22	0.32 ± 0.03	9	-1.19	0.24	-
Triglyceride	1.1 ± 0.1	18	1.1 ± 0.2	9	-0.02	0.99	Date (+)**
Glycerol	0.6 ± 0.0	14	0.5 ± 0.1	9	-1.19	0.25	Sex (F >M) **, Mass (+) *
Total antioxidant capacity	0.42 ± 0.03	23	0.45 ± 0.04	11	0.26	0.80	-
Total oxidative status	0.88 ± 0.10	23	0.86 ± 0.15	11	-0.12	0.91	-

†Determined at a commercial laboratory. Models include a factor to control for the identity of the technician who processed the sample.

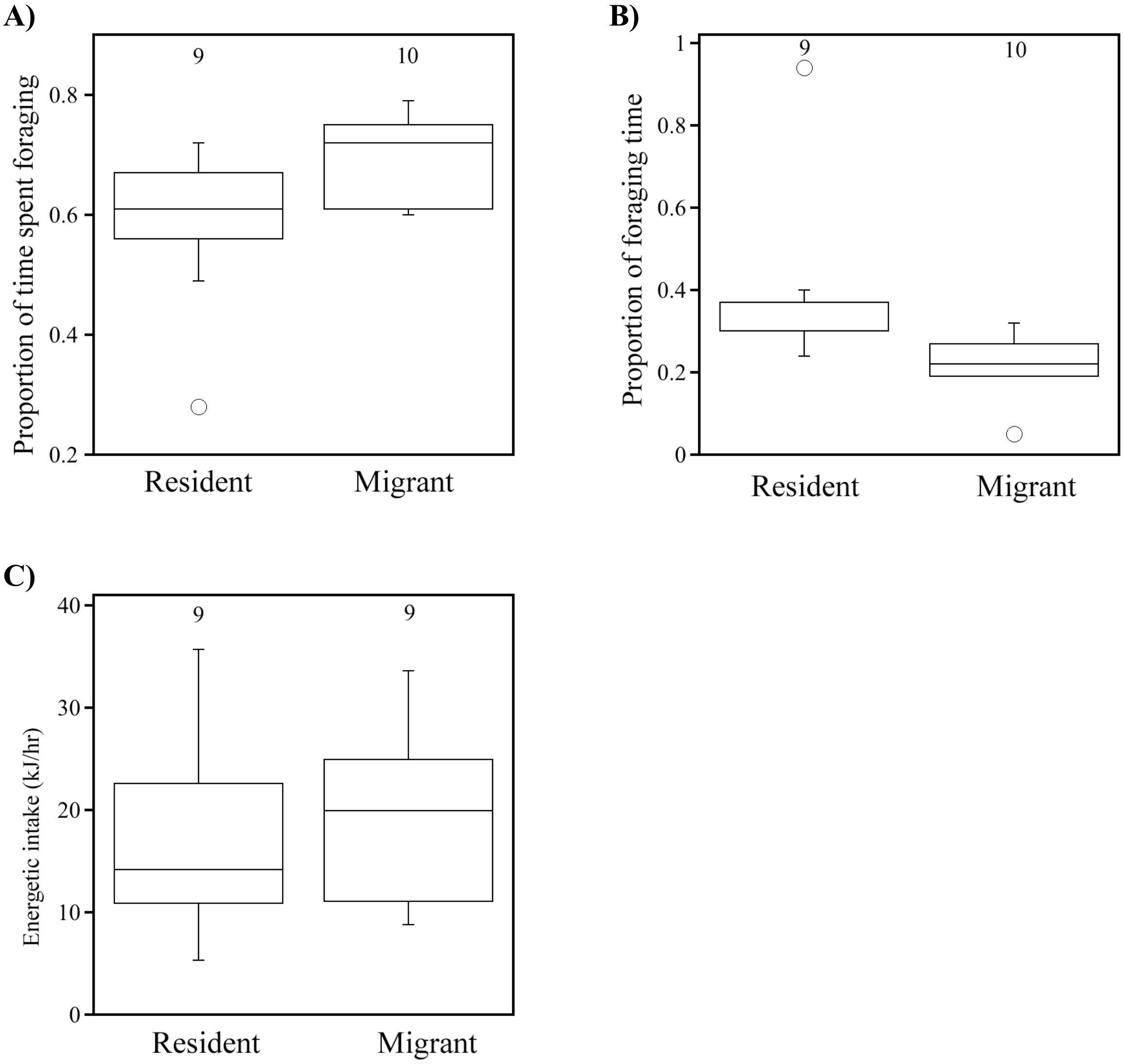

Figure 4.1: Foraging behaviour and energetic intake of migrant and resident wintering American dippers Boxplots show median, 1st and 3rd quartiles, minimum and maximum values (and outliers). A) Percent of total time spent foraging, p = 0.04. B) Present of time foraging using shallow-water methods, p = 0.04. C) Calculated energetic intake, controlling for date effects, p = 0.50. Numbers indicate sample size for each category. For both A and B, results do not substantially differ if outliers are excluded.

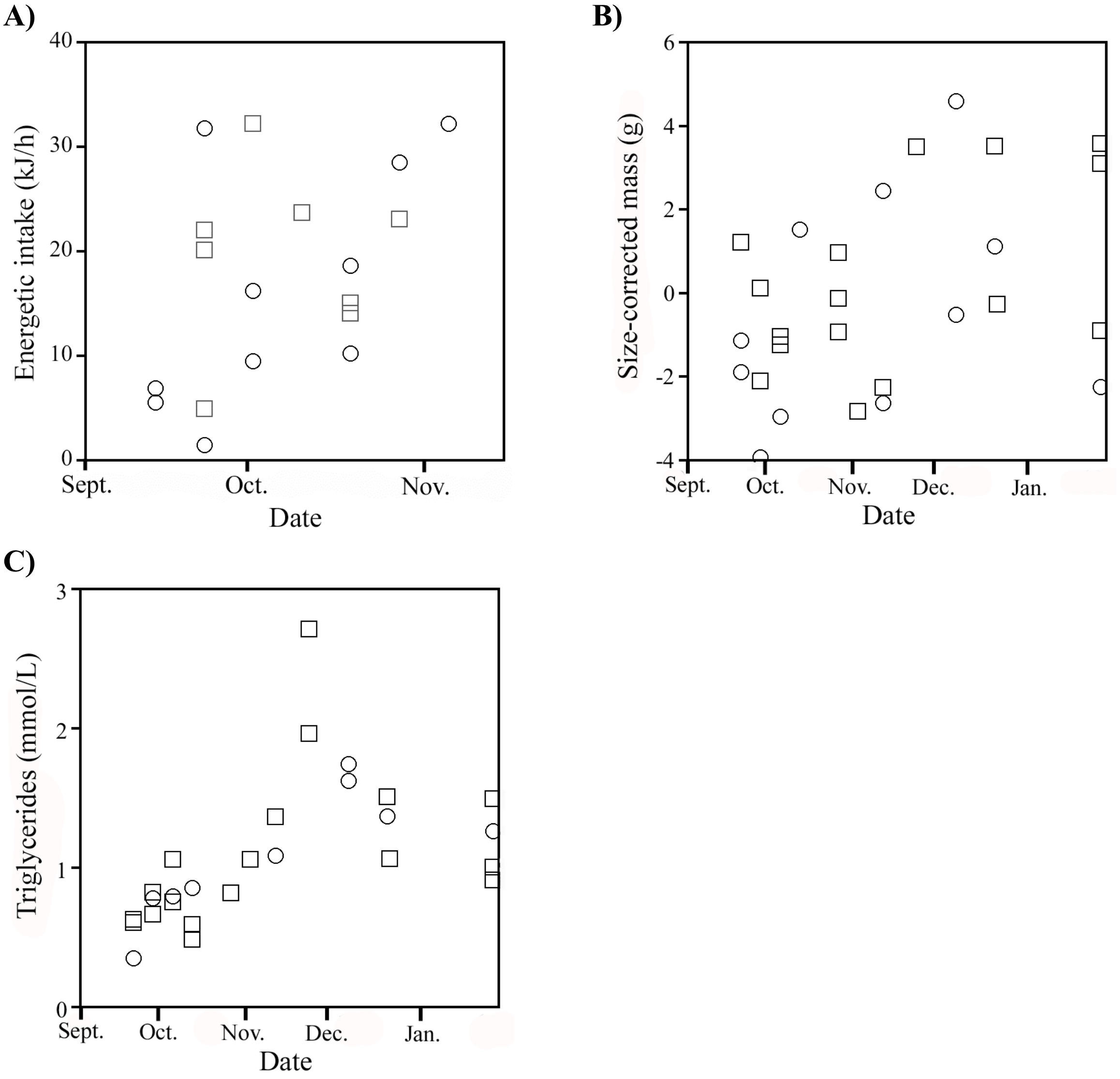

Figure 4.2: Seasonal changes in behaviour and physiology of migrant and resident wintering American dippers.
A) Energetic intake, p = 0.06. B) Size-corrected mass (see text for details of calculation), p = 0.04. C) Triglycerides, p > 0.01. Circles represent residents and squares represent migrants.

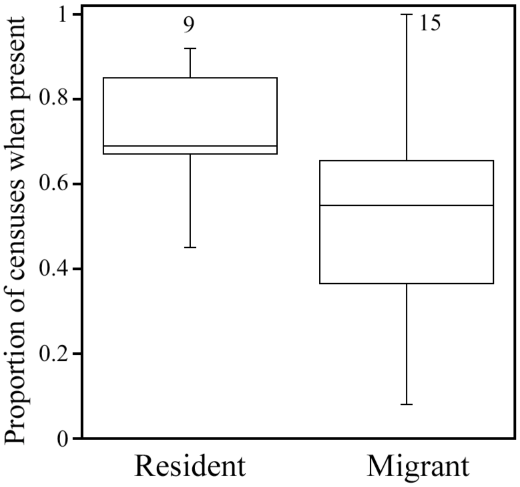

Figure 4.3: Site fidelity in wintering migrant and resident American dippers.
Proportion of censuses when individuals were observed at their wintering site. See text for details of calculation. $p < 0.001$. Numbers indicate number of individuals in each category.

CHAPTER 5: CONCLUSIONS

Migration is a widespread phenomenon in birds, but the processes underlying the evolution of migration are still under debate (Bell 2000, Berthold 1999, 2001, Rappole 1995). Understanding the costs and benefits associated with migration is a key step towards understanding the evolution of this behaviour. Species that vary in migratory habit, such as partial migrants, offer a unique opportunity to investigate these costs and benefits by allowing direct comparison of migratory and sedentary individuals.

I used a population of partially migratory American dipper, *Cinclus mexicanus,* to investigate costs and benefits of migration. This population consists of altitudinal-migrant and sedentary (resident) individuals, and previous work has identified that migrant and resident individuals differ in both reproductive success and survival. On average migrants fledge fewer young than residents, but this decrease in reproductive success is partially offset by their higher annual survival (Gillis *et al.* 2008). The migrant's lower reproductive success appears to result primarily from their later initiation of breeding, which decreases their probability of raising a second brood (Morrissey 2004). However, the cause underlying the difference in survival is unknown.

I first tested if the difference in reproductive success could be explained by age effects (see Chapter Two). Age is known to affect reproduction in a wide variety of birds (Clutton-Brock 1988, Sæther 1990), and the age of breeding individuals had not previously been considered in this population. I found that while female age has a strong effect on reproductive success, with older females fledging more young than yearling females, this age effect does not explain the migrant-resident difference in reproductive success.

Subsequent chapters tested two hypotheses relating to the observed survival difference between migrants and residents. Firstly, migrants and residents appear to be trading-off reproduction and survival, and I investigated if this apparent trade-off is an expression of a physiologically-mediated cost of reproduction (see Chapter Three). I found no evidence that differences in reproductive effort between the two groups led to differences in physiological condition at the end of breeding which could affect subsequent survival, suggesting that this apparent trade-off is not an expression of a physiologically-mediated cost of reproduction. My data does not demonstrate that the cost of reproduction does not occur in this population at the individual level, but indicates that a physiologically-mediated cost of reproduction does not underlie the greater survival of migrants as a group.

My second hypothesis about the migrant-resident survival difference concerned the effects of behaviour on survival during the winter. Resident individuals remain on their territories year-round, while migrants move between high-elevation breeding territories and low-elevation wintering areas. Territory ownership can carry costs, such as reduced anti-predator vigilance (Dunn *et al*. 2004) and periodic food shortages or constrained ability to track food supply (Brown and Sherry 2008, McFarland 2002, Pérez-Tris and Tellería 2002). I tested if remaining on a multi-purpose, year-round territory imposed constraints on the foraging behaviour, energetic intake, and site fidelity of resident individuals during winter, and if this potential constraint resulted in residents being in poorer physiological state (see Chapter Four). While I did observe differences in foraging behaviour, they did not result in a lower energetic intake for residents. However, migrants appear to use larger wintering home ranges, increasing their spatial flexibility. While these differences in behaviour did not result in poorer physiological state for residents, the reduced spatial flexibility of residents may put them at greater risk of dying during extreme events that restrict food supply, such as flooding.

Overall, my data is consistent with earlier observations (Gillis *et al.* 2008) of higher reproductive success among residents and higher annual survival rates for migrants. In this system, migration incurs a cost in terms of lower reproductive success, due to later initiation of breeding. However, migration also carries a benefit in terms of increased annual survival. I found no evidence that this increased survival is an expression of a physiologically-mediated cost of reproduction, but differences in winter behaviour are suggestive. Migrants may be benefiting from their greater spatial flexibility, which could allow better response to changes in food resources, particularly during poor conditions (Brown and Sherry 2008, Pérez-Tris and Tellería 2002).

While migrants may be benefiting from increased spatial flexibility, my data is merely suggestive, rather than conclusive. If residents are paying a cost for remaining near and defending a nesting site year-round, it is expected that resident individuals will spend more time and energy engaging in aggressive or territorial behaviour than migrants or juveniles. Detailed observations on interactions between residents and other individuals wintering on or near the resident's territory would be beneficial. In addition, if residents are constrained to remain on their territory, they should be more reluctant to leave during poor conditions and thus respond more slowly than migrants to food shortages, ice cover, or severe flooding. They may also not move as far, frequently visit or be quicker to return to their usual territory, or be less efficient at finding food when off-territory. Detailed spatial data from radio transmitters, combined with careful behavioural observations, particularly during stressful events such as extremely cold weather or flooding, would help address these questions.

There are other questions about this dipper system that remain unanswered. The most intriguing of these is the mechanism that determines which migratory strategy a juvenile dipper will employ. In systems where migratory habit is variable, the strategy an individual employs is thought to be condition-dependent or under genetic control (reviewed in Lundberg 1988). There is no evidence that the migratory strategy of dippers is under strict genetic control, as the migratory strategy of the parents does not determine the strategy of the offspring (Gillis *et al.* 2008), nor is there any morphological variation associated with flight efficiency between the two strategies (migratory individuals often have longer and more pointed wings for greater flight efficiency in partial migrant populations; Green *et al.* 2009). In cases where strategy is conditional, it is generally the subdominant individuals that migrate. The migratory portion of the population is thus often biased towards females or juveniles, and individuals may change strategy during their lifetime (e.g. Adriaensen and Dhont 1990, Herremans 1994, Nilsson *et al.* 2008, Rabenold and Rabenold 1985, Schwabl 1983). However, dippers in this population do not switch migratory strategy and there is no difference in morphology or size between migrant and resident individuals (Gillis *et al.* 2008, Green *et al.* 2009), indicating that age and size do not play a role in determining dominance. While there are some differences in foraging behaviour between adult migrants and residents (Chapter Four), preliminary data indicates that the foraging behaviour of juveniles during their first winter appears to match that of residents (I. Whitehorne, unpublished data), suggesting that these differences arise after individuals determine their migratory strategy. What determines the migratory strategy a juvenile dipper will employ is still unknown and is deserving of further investigation. Competition for resident territories could be created by building artificial nesting substrates in suitable low-elevation areas that currently lack nesting sites. Careful monitoring of the physiological state, hormone levels and dominance interactions of dippers in the area (both juveniles and wintering migrants) through winter and establishment of a breeding pair could shed light on this persistent question.

REFERENCES

Adamo, S. A. 2004. How should behavioural ecologists interpret measurements of immunity? Anim. Behav. 68: 1443-1449

Adriaensen, F., and A. A. Dhont. 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. J. Anim. Ecol. 59(3): 1077-1090.

Alonso-Alvarez, C., S. Bertrand, G. Devevey, J. Prost, B. Faivre and G. Sorci. 2004. Increased susceptibility to oxidative stress as a proximate cost of reproduction. Ecol. Lett. 7: 363-368

Apanius, V., and I. C. T. Nisbet. 2006. Serum immunoglobulin G levels are positively related to reproductive performance in a long-lived seabird, the common tern (*Sterna hirundo*). Oecologia. 147: 12-23

Badyaev, A. V., and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. Ecology. 82(10): 2948-2960

Bakus, 1959a. Observations on the life history of the dipper in Montana. Auk. 76: 190-207

Bakus, 1959b. Territoriality, movements and population density of the dipper in Montana. Condor. 61: 410-425

Balbontín, J., I. G. Hermosell, A. Marzal, M. Reviriego, F. de Lope, and A. P. Møller. 2007. Age-related change in breeding performance in early life is associated with an increase in competence in the migratory barn swallow *Hirundo rustica*. J. Anim. Ecol. 76: 915-925

Barbraud, C. and H. Weimerskirch. 2005. Environmental conditions and breeding experience affect costs of reproduction in blue petrels. Ecology. 86(3): 682-692

Beauchamp, G. 1998. The effect of group size on mean food intake in birds. Biol. Rev. 73: 449-472

Bell, C. P. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. J. Avian Biol. 31: 258-265

Berthold, P. 1999. A comprehensive theory for the evolution, control and adaptability of avian migration. Ostrich. 70(1): 1-11

Berthold, P. 2001. Bird migration: a general survey, 2nd ed (*Trans. by*: H-G. Bauer and V. Westhead). Oxford University Press, Oxford.

Berthold, P., and U. Querner. 1981. Genetic basis of migratory behaviour in European warblers. Science. 212(4490): 77-79

Biebach, H. 1983. Genetic determination of partial migration in the European robin (*Erithacus rubecula*). Auk. 100:601-606

Boldt, J. L., and L. J. Haldorson. 2004. Size and condition of wild and hatchery pink salmon juveniles in Prince William Sound, Alaska. Trans. Am. Fish. Soc. 133: 173-184

Bourgeon, S., J. Martínez, F. Criscuolo, Y. Le Maho, and T. Raclot. 2006. Fasting-induced changes of immunological and stress indicators in breeding female eiders. Gen. Comp. Endocrinol. 147:336-342

Brey, T., H. Rumhor, and S. Ankar. 1988. Energy content of macrobenthic invertebrates: general conversion factors from weight to energy. J. Exp. Mar. Biol. Ecol. 117:271-278

Brodin, A. 2005. Mechanisms of cache retrieval in long-term hoarding birds. J. Ethol. 23:77-83

Brodin, A. 2007. Theoretical models of adaptive energy management in small wintering birds. Phil. Trans. R. Soc. B. 362: 1857-1871

Brown, D. R., and J. A. Long. 2007. What is a winter floater? Causes, consequences and implications for habitat selection. Condor. 109: 548-565

Brown, D. R., and T. W. Sherry. 2008. Alternative strategies of space use and response to resource change in a wintering migrant songbird. Behav. Ecol. 19(6): 1314-1325

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. Springer, New York, N.Y.

Caro, S. P., A. Charmantier, M. M. Lambrechts, J. Blondel, J. Balthazart, and T. D. Williams. 2009. Local adaptation of timing of reproduction: females are in the driver's seat. Funct. Ecol. 23(1): 172-179

Chan, K. 2001. Partial migration in Australian landbirds: a review. Emu. 101: 281-292

Chingbu, P. 2001. Occurrence and distribution of *Salmincola californiensis* (Copepoda: Lernaeopodidae) on juvenile sockeye salmon (*Oncorhynchus nerka*) in Lake Washington. J. Freshw. Ecol. 16(4): 615-620

Christe, P., F. de Lope, G. González, N. Saino, A. P. Møller. 2001. The influence of environmental condition on immune responses, morphology and recapture probability of nestling house martins (*Delchion urbica*). Oecologia. 126: 333-338

Cichon, M. 2001. Body-mass changes in female collared flycatchers: state-dependent strategy. Auk. 118(2): 550-552

Clinchy, M., L. Zanette, R. Boonstra, J. C. Wingfield, and J. N. M. Smith. 2004. Balancing food and predator pressure induces chronic stress in songbirds. Proc. R. Soc. Lond. B. 271: 2473-2479

Clutton-Brock, T.H (*ed*). 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, IL.

Costantini, D., G. Dell'Ariccia, and H-P. Lipp. 2008. Long flights and age affect oxidative status of homing pigeons (*Columbia livia*). J. Exp. Biol. 211: 377-381

Curio, E. 1983. Why do young birds reproduce less well? Ibis. 125: 400-404

D'Amico, F., and G. Hémery. 2007. Time-activity budgets and energetics of dipper *Cinclus cinclus* are dictated by temporal variability of river flow. Comp. Biochem. Physiol. A. 148: 811-829

Davis, A. K., D. L. Maney, and J. C. Maerz. 2008. The use of leucocyte profiles to measure stress in vertebrates. Funct. Ecol. 22: 760-772

Dawson, R. D., and G. R Bortolotti. 1997. Are avian hematocrits indicative of condition? American kestrels as a model. J. Wildl. Manage. 61(4): 1297-1306

de Vries, J., and M. R. van Eerden. 1995. Thermal conductance in aquatic birds in relation to the degree of water contact, body mass and body fat: energetic implications of living in a strong cooling environment. Physiol. Zool. 68(6): 11423-1163

Deerenberg, C., V. Arpanius, S. Daan and N. Bos. 1997. Reproductive effort decreases antibody responsiveness. Proc. R. Soc. Lond. B. 264:1021-1029

Dein, J. 1986. Hematology. *In* Clinical avian medicine and surgery, including aviculture (G. J. Harrison and W. R. Harrison, eds.). W. B. Saunders Company, London. pp174-191

Dempson, J. B., C. J. Schwarz, M. Shears, and G. Furey. 2004. Comparative proximate body composition of Atlantic salmon with emphasis on parr from fluvial and lacustrine habitats. J. Fish Biol. 64: 1257-1271

Desrochers, A. 1992. Age-related differences in reproduction by European blackbirds: restraint or constraint? Ecology. 73(3): 1128-1131

Desrochers, A., and R. D. Magrath. 1993. Age-specific fecundity in European blackbirds (*Turdus merula*): individual and population trends. Auk. 110(2): 255-263

Dhabhar, F. S., A. H. Miller, B. S. McEwen, and R. L. Spencer. 1995. Effects of stress on immune cell distribution: dynamics and hormonal mechanisms. J. Immunol. 154: 5511-5527

Donnelly, R. E., and K. A. Sullivan. 1998. Foraging proficiency and body condition of juvenile American dippers. Condor. 100: 385-388

Dow, H. and S. Fredga. 1984. Factors affecting reproductive output of the goldeneye duck *Bucephala clangula*. J. Anim. Ecol. 53: 679-692

Dunn, M., M. Copelston, and L. Workman. 2004. Trade-offs and seasonal variation in territorial defence and predator evasion in the European robin *Erithacus rubecula*. Ibis. 146: 77-84

Eguchi, K. 1990. The choice of foraging methods of the brown dipper, *Cinclus pallasii*. J. Ethol. 8: 121-127

Ens, B. J., F.J. Weissing, and R. H. Drent. 1995. The despotic distribution and deferred maturity: two sides of the same coin. Am. Nat. 146(4): 625-650

Erel, O. 2004. A novel automated direct measurement method for total antioxidant capacity using a new generation, more stable ABTS radical cation. Clin. Biochem. 37:277-285

Erel, O. 2005. A new automated colorimetric method for measuring total oxidant status. Clin. Biochem. 38:1103-1111

Espie, R. H. M., L. W. Oliphant, P. C. James, I. G. Warkentin, and D. J. Lieske. 2000. Age-dependant breeding performance in merlins (*Falco columbarius*). Ecology. 81(12): 3404-3415

Evans, P. R. 1969. Winter fat deposition and overnight survival of yellow buntings (*Emberiza citrinella* L.). J. Anim. Ecol. 38: 415-423

Finkel, T., and N. J. Holbrook. 2000. Oxidants, oxidative stress and the biology of ageing. Nature. 408(6809): 239-247

Fleming, I. A., and M. R. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in pacific salmon. Ecology. 71(1): 1-11

Forslund, P., and T. Pärt. 1995. Age and reproduction in birds—hypotheses and tests. Trends Ecol. Evol. 10(9): 374-378

Gabrielson, I. N., and F. C. Lincoln. 1959. The birds of Alaska. Stackpole Co. Harrisburg, Pennsylvania; and Wildlife Management Institute, Washington, DC. 922pp.

Gillis, E. A., D. J. Green, H. A. Middleton, and C. A. Morrissey. 2008. Life history correlates of alternative migratory strategies in American dippers. Ecology. 89(6): 1687-1695

Gonzalez, G., G. Sorci, A. P. Møller, P Ninni, C. Haussy, and F. de Lope. 1999. Immunocompetence and condition-dependant sexual advertisement in male house sparrows (*Passer domesticus*). J. Anim. Ecol. 68: 1225-1234

González-Solís, J., P. H. Becker, L. Jover, and X. Ruiz. 2004. Individual changes underlie age-specific pattern of laying date and egg-size in female common terns (*Sterna hirundo*). J. Ornithol. 145: 129-136

Gosler, A. G. 2002. Strategy and constraint in the winter fattening response to temperature in the great tit *Parus major*. J. Anim. Ecol. 71: 771-779

Green, D. J. 2001. The influence of age on reproductive performance in the brown thornbill. J. Avian Biol. 32: 6-14

Green, D. J., I. B. J. Whitehorne, A. Taylor and E. L. Drake. 2009. Wing morphology varies with age but not migratory habit in American dippers. Wilson J. Ornith. 121(1): 141-147

Gross, W. B., and H. S. Siegel. 1983. Evaluation of the heterophil/lymphocyte ratio as a measure of stress in chickens. Avian Dis. 27(4): 972-979

Guglielmo, C. G., D. J. Cerasale, and C. Eldermire. 2005. A field validation of plasma metabolite profiling to assess refuelling performance of migratory birds. Physiol. Biochem. Zool. 78(1): 116-125

Guglielmo, C. G., P. D. O'Hara, and T. D. Williams. 2002. Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living Western sandpipers (*Calidris mauri*). Auk. 119(2): 437-445

Gustafsson, L., D. Nordling, M. A. Andersson, B. C. Sheldon, and A. Qvarnstrom. 1994. Infectious diseases, reproductive effort and the cost of reproduction in birds. Phil. Trans. R. Soc. Lond. 346(1317): 323-331

Gustafsson, L., and W. J. Sutherland. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature. 335: 813-815

Hamann, J., and F. Cooke. 1987. Age effects on clutch size and laying dates of individual female lesser snow geese *Anser caerulescens*. Ibis. 129: 527-532

Harshmann, L. G. and A. J. Zera. 2007. The cost of reproduction: the devil in the details. Trends Ecol. Evol. 22(2): 80-86

Hatch, M. I., and D. F. Westneat. 2007. Age-related patterns of reproductive success in house sparrows *Passer domesticus*. J. Avian Biol. 38: 603-611

Hendry, A. P., and O. K. Berg. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. Can. J. Zool. 77: 1663-1675

Herremans, M. 1994. Partial migration in the masked weaver *Ploceus velatus* in southeastern Botswana. Ostrich. 65: 79-85

Hogstad, O. 2003. Strained energy budget of winter floaters in the willow tit as indicated by ptilochronology. Ibis. 145: E19-E23

Hõrak, P., I. Ots, and A. Murumägi. 1998. Haematological health state indices of reproducing great tits: a response to brood size manipulation. Funct. Ecol. 12: 750-756

Huertas, D. L., and J. A. Diaz. 2001. Winter habitat selection by a montane forest bird assemblage: the effects of solar radiation. Can. J. Zool. 79: 279-284

Hylton, R. A., P. C. Frederick, T. E. de la Fuente, and M. G. Spalding. 2006. Effects of nestling health on postfledging survival of wood storks. Condor. 108: 97-106

Ilmonen, P., T. Taarna, and D. Hasselquist. 2000. Experimentally activated immune defence in female pied flycatchers results in reduced breeding success. Proc. R. Soc. Lond. B. 267: 665-670

Jenni, L. 1991. Microclimate of roost sites selected by wintering bramblings, *Fringilla montifringilla*. Ornis Scand. 22: 327-334

Jenni-Eiermann, S. and L. Jenni. 1994. Plasma metabolite levels predict individual body-mass changes in a small long-distance migrant, the garden warbler. Auk. 111(4): 888-899

King, D. G., A. Grass, and K. Summers. 1973. Observations of the dipper in the Skagit valley of British Columbia. Murrelet. 54(2): 16-19

Kingery, H. E. 1996. American Dipper (*Cinclus mexicanus*). No. 229 *In* The Birds of North America (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA., and the American Ornithologists' Union, Washington, DC.

Kooyman, G. L., R. L. Gentry, W. P. Bergman, and H. T. Hammel. 1976. Heat loss in penguins during immersion and compression. Comp. Biochem. Physiol. 54A: 75-80

Lessells, C. M. 1991. The evolution of life histories. *In* Behavioural ecology: An evolutionary approach, 3rd ed. (J. R. Krebs and N. B. Davies, eds.). Blackwell Scientific Publications, Oxford. pp32-68

Lindén, M., L. Gustafsson, and T. Pärt. 1992. Selection on fledgling mass in the collared flycatcher and the great tit. Ecology. 73(1): 336-343

Loegring, J. P., and R. G. Anthony. 2006. Nest-site selection and productivity of American dippers in the Oregon coast range. Wilson J. Ornith. 118(3): 281-294

Loison, A., B-E. Sæther, K. Jerstad, and O. W. Røstad. 2002. Disentangling the sources of variation in the survival of the European dipper. J. App. Stat. 29: 289-304

Low, M., T. Pärt, and P. Forslund. 2007. Age-specific variation in reproduction is largely explained by the timing of territory establishment in the New Zealand stitchbird *Notiomystis cincta*. J. Anim. Ecol. 76(3): 459-470

Lozano, G. A., S. Perreault, and R. E. Lemon. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. J. Avian Biol. 27(2): 164-170

Lundberg, P. 1988. The evolution of partial migration in birds. Trends Ecol. Evol. 3(7): 172-175

Lundberg, P., A. Bergman, and H. Olsson. 1981. On the ecology of wintering dippers (*Cinclus cinclus*) in northern Sweden. J. Ornithol. 122: 163-172

Martin, K. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. Am. Zool. 35:340-348

Martin, L. B., M. Pless, J. Svoboda, and M. Wikelski. 2004. Immune activity in temperate and tropical house sparrows: a common garden experiment. Ecology. 85(8): 2323-2331

Martínez, J., G. Tomás, S. Merino, E. Arriero and J. Moreno. 2003. Detection of serum immunoglobulins in wild birds by direct ELISA: a methodological study to validate the technique in different species using antichicken antibodies. Funct. Ecol. 17: 700-706

Mauck, R. A., C. E. Huntington, and T. C. Grubb. 2004. Age-specific reproductive success: evidence for the selection hypothesis. Evolution. 58(4): 880-885

McFarland, D. C. 2002. Non-breeding territoriality in the New Holland Honeyeater, *Phylidonyris novaehollandiae*, in an unpredictable environment — short-term energy costs for possible long-term reproductive benefits. Emu. 102: 315-321

Middleton, H. A., C. A. Morrissey, and D. J. Green. 2006. Breeding territory fidelity in a partial migrant, the American dipper *Cinclus mexicanus*. J. Avian Biol. 37: 169-178

Monaghan, P., and G. Nager. 1997. Why don't birds lay more eggs? Trends Ecol. Evol. 12(7): 270-274

Morales, J., J. Moreno, S. Merino, G. Tomás, J. Martínez, and L. Z. Garamszegi. 2004. Associations between immune parameters, parasitism, and stress in breeding pied flycatcher (*Ficedula hypoleuca*) females. Cdn. J. Zool. 82: 1484-1492

Moreno, J., A. de León, J. A. Fargallo, and E. Moreno. 1998. Breeding time, health and immune response in the chinstrap penguin *Pygoscelis antarctica*. Oecologia. 115: 312-319

Moreno, J., J. J. Sanez, and E. Arriero. 1999. Reproductive effort and T-lymphocyte cell-mediated immunocompetence in female pied flycatchers *Ficedula hypoleuca*. Proc. R. Soc. Lond. B. 266: 1105-1109

Moreno, J., P. Yorio, P. Garcia-Borboroglu, J. Potti and S. Villar. 2002. Health state and reproductive output in Magellanic penguins (*Spheniscus magellanicus*). Ethology Ecol. Evol. 14: 19-28

Morrissey, C. A. 2004. Effect of altitudinal migration within a watershed on the reproductive success of American dippers. Can. J. Zool. 82(5): 800-807

Morrissey, C. A., L. Bendell-Young, and J. E. Elliot. 2004. Seasonal trends in population density, distribution, and movement of American dippers within a watershed of southwestern British Columbia, Canada. Condor. 106: 815-825

Muller, F. L., M. S. Lustgarden, Y. Jang, A. Richardson, and H. Van Remmen. 2007. Trends in oxidative aging theories. Free Radic. Biol. Med. 43: 477-503

Newton, I. 1998. Population limitation in birds. Academic Press, London.

Nilsson, A. L. K., T. Alerstam, and J-Å. Nilsson. 2008. Diffuse, short and slow migration among blue tits. J. Ornithol. 149(3): 365-373

Nol, E., and J. N. M. Smith. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. J. Anim. Ecol. 56(1): 301-313

Norberg, R. Å. 1981. Temporary weight decrease in breeding birds may result in more fledged young. Am. Nat. 118(6): 838-850

Nordling, D., M. Andersson, S. Zohari, and L. Gustafsson. 1998. Reproductive effort reduces specific immune response and parasite resistance. Proc. R. Soc. Lond. B. 265: 1291-1298

Ollason, J. C. and G. M. Dunnett. 1988. Variation in breeding success in fulmars. *In* Reproductive success: studies of individual variation in contrasting breeding systems (T. H. Clutton-Brock, ed.). University of Chicago Press, Chicago. pp. 263-278

Orell, M., and E. J. Belda. 2002. Delayed cost of reproduction and senescence in the willow tit *Parus montanus*. J. Anim. Ecol. 71: 55-64

Ormerod, S. J., and S. J. Tyler. 1990. Assessment of body condition in dippers *Cinclus cinclus*: potential pitfalls in the derivation and use of condition indices based on body proportions. Ring. Migr. 11: 31-41

Ots, I., and P. Hõrak. 1996. Great tits *Parus major* trade health for reproduction. Proc. R. Soc. Lond. B. 263: 1443-1447

Ots, I., A. Murumägi, and P. Hõrak. 1998. Haematological health state indices of reproducing great tits: methodology and sources of natural variation. Funct. Ecol. 12(4): 700-707

Owen, J.C., and F. R. Moore. 2006. Seasonal differences in immunological condition of three species of thrushes. Condor. 108: 389-398

Owen, J. C., M. K. Sogge, and M. D. Kern. 2005. Habitat and sex differences in physiological condition of breeding southwestern willow flycatchers (*Empidonax traillii extimus*). Auk. 122(4): 1261-1270

Perdeck, A. C., and A. J. Cavé. 1992. Laying date in the coot: effects of age and mate choice. J. Anim. Ecol. 61(1): 13-19

Pérez-Tris, J., S. Bensch, R. Carbonell, A. J. Helbig, and J. L. Tellería. 2004. Historical diversification of migration patterns in a passerine bird. Evolution. 58(8): 1819-1832

Pérez-Tris, J., and J. L. Tellería. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. J. Anim. Ecol. 71: 211-224

Piersma, T., A. Koolhaas, A. Dekinga and E. Gwinner. 2000. Red blood cell counts in sandpipers (*Philomachus pugnax, Caldris canutus*): effects of captivity, season, nutritional status, and frequent bleedings. Can. J. Zool. 78(8): 1349-1355

Price, F. E., and C. E. Bock. 1983. Population ecology of the dipper (*Cinclus mexicanus*) in the Front Range of Colorado. Studies in avian biology, no. 7. Cooper Ornithological Society and Allen Press Inc., Lawrence, KS.

Pugesek, B. H. 1987. Age-specific survivorship in relation to clutch size and fledgling success in California gulls. Behav. Ecol. Sociobiol. 21: 217-221

Pulido, F. 2007. The genetics and evolution of avian migration. Bioscience. 57(2): 165-174

Pyle, P. 1997. The identification guide to North American birds: part 1. Slate Creek Press, Bolinas, CA.

Rabenold, K. N., and P. P. Rabenold. 1985. Variation in altitudinal migration, winter segregation, and site tenacity in two subspecies of dark-eyed juncos in the southern Appalachians. Auk. 102: 805-819

Rappole, J.H. 1995. The ecology of migrant birds: a neotropical perspective. Smithsonian Institution Press, Washington, DC.

Reid, J. M., E. M. Bignal, S. Bignal, D. I. McCracken, and P. Monaghan. 2003. Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. J. Anim. Ecol. 72: 765-776

Reznick, D., L. Nunney and A. Tessier. 2000. Big houses, big cars, superfleas and the costs of reproduction. Trends Ecol. Evol. 15(10): 421-425

Rose, M. E., P. Hesketh, and B. Olgivie. 1979. Peripheral blood leukocyte response to coccoidal infection: a comparison of the response in rats and chickens and its correlation with resistance to reinfection. Immunology. 36: 71-79

Ruiz, G., M. Rosenmann, F. F. Novoa, and P. Sabat. 2002. Hematological parameters and stress index in rufous-collared sparrows dwelling in urban environments. Condor. 104: 162-166

Sæther, B-E. 1990. Age-specific variation in reproductive performance of birds. *In* Current ornithology, Vol. 7 (D. M. Power, ed.). Plenum Press, New York, NY. pp. 251-284.

Sæther, B-E., J. Tufto, S. Engen, K. Jerstad, O. W. Røstad, and J. E. Skåtan. 2000. Population dynamical consequences of climate change for a small temperate songbird. Science. 287(5454): 854-856

Saino, N., A. M. Bolzern, and P. A. Møller. 1997a. Immunocompetence, ornamentation, and viability of male barn swallows (*Hirundo rustica*). Proc. Nat. Acad. Sci. USA. 94: 549-552

Saino, N., J. J. Cuvero, M. Krivacek, F. de Lope, and A. P. Møller. 1997b. Experimental manipulation of tail ornament size affects the hematocrit of male barn swallows. Oecologia. 110: 186-190

Salgado-Ortiz, J., P. P. Marra, T. S. Sillett, and R. J. Robertson. 2008. Breeding ecology of the mangrove warbler (*Dendroica petechia bryanti*) and comparative life history of the yellow warbler subspecies complex. Auk. 125(2): 402-410

Schaub, M., and L. Jenni. 2001. Variation of fuelling rates among sites, days and individuals in migrating passerine birds. Funct. Ecol. 15(5): 584-594

Schwabl, V. H. 1983. Ausprägung und Bedeutung des Teilzugverhaltens einer südwestdeutschen Population der Amsel *Turdus merula* (Expression and significance of the winter strategies in a partially migratory population of European blackbirds). J. Ornithol. 124(2): 101-116. *German with English summary.*

Sheldon, B. C., and S. Verhulst. 1996. Ecological immunity: costly parasite defences and trade-offs in evolutionary ecology. Trend. Ecol. Evol. 11(8): 317-321

Smits, J. E., and T. D. Williams. 1999. Validation of immunotoxicology techniques in passerine chicks exposed to oil sands tailings water. Ecotoxicol. Environ. Saf. 44: 105-112

Stahel, C. D., and S. C. Nicol. 1982. Temperature regulation in the little penguin, *Eudyptula minor*, in air and water. J. Comp. Physiol. B. 148: 93-100

Stearns, S. C. 1989. Trade-offs in life-history evolution. Funct. Ecol. 3(3): 259-268

Suárez, F., J. Traba, and H. Herranez. 2005. Body mass changes in female tawny pipits *Anthus campestris* during the nestling stage. J. Ornithol. 146: 372-376

Terrill, S. B., and K. P. Able. 1988. Bird migration terminology. Auk. 105: 205-206

Thut, R. 1970. Feeding habits of the dipper in southwestern Washington. Condor. 72: 234-235

Tomas, G., S. Merino, J. Moreno, J. Morales, and J. Martinez-de la Puente. 2007. Impact of blood parasites on immunoglobulin level and parental effort: a medication field experiment on a wild passerine. Funct. Ecol. 21: 125-133

Tyler, S. J., and S. J. Ormerod. 1994. The dippers. Academic Press Inc., San Diego, CA.

van de Pol, M., and S. Verhulst. 2006. Age-dependent traits: a new statistical model to separate within- and between-individual effects. Am. Nat. 167(5): 766-773

van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. Am. Nat. 128(1): 137-142

Visser, M. E., and C. M. Lessells. 2001. The costs of egg production and incubation in great tits (*Parus major*). Proc. R. Soc. Lond. B. 268: 1271-1277

Warne, R. W., and E. L Charnov. 2008. Reproductive allometry and the size-number trade-off for lizards. Am. Nat. 172(3): E80-E92

Wheelwright, N. T., and C. B. Schultz. 1994. Age and reproduction in savannah sparrows and tree swallows. J. Anim. Ecol. 63(3): 686-702

Whitney, M., and G. Whitney. 1972. A study of dippers on the St. Vrain Creek, Colorado. Western Bird Bander. 47: 3-9

Wiersma, P., C. Selman, J. R. Speakman and S. Verhulst. 2004. Birds sacrifice oxidative protection for reproduction. Proc. R. Soc. Lond. B. (Suppl). 271: S360-S363

Wiktander, U., O. Olsson, and S. G. Nilsson. 2001. Age and reproduction in lesser spotted woodpeckers (*Dendrocopos minor*). Auk. 118(3): 624-635

Williams, J. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100(916): 687-690

Williams, T. D., J. K. Christians, J. J. Aiken, and M. Evanson. 1999a. Enhanced immune function does not depress reproductive output. Proc. R. Soc. Lond. B. 266: 753-757

Williams, T. D., C. G. Guglielmo, O. Egeler and C. J. Martyniuk. 1999b. Plasma lipid metabolites provide information on mass change over several days in captive Western sandpipers. Auk. 116(4): 994-1000

Willson, M. F., and K. M. Hocker. 2008. American dippers wintering near Juneau, Alaska. Northwestern Naturalist. 89(1): 24-32

Wilson, J. D. 1996. The breeding biology and population history of the dipper *Cinclus cinclus* in a Scottish river system. Bird Study. 43: 108-118

Young, B. E. 1996. An experimental analysis of small clutch size in tropical house wrens. Ecology. 77(2): 472-488