Nutrient acquisition by female Harlequin Ducks prior to spring migration and reproduction: evidence for body mass optimization

Jeanine C. Bond and Daniel Esler

Abstract: We analysed variation in body mass of adult female Harlequin Ducks (*Histrionicus histrionicus* (L., 1758)) on coastal wintering sites in southern British Columbia, Canada, to investigate nutrient acquisition prior to migration and reproduction. On average, female mass increased by 7% from late winter to premigration; however, the chronology of mass gain varied depending on prey type. Females feeding on superabundant roe from spawning Pacific herring (*Clupea pallasii* Valenciennes, 1847) became considerably heavier than they had been before the herring spawning period (March) and appeared to be heavier than females eating marine invertebrates such as crabs, limpets, and snails during the herring spawning period. By mid-April, (L., prior to migration, females at all sites had similar body masses,Histrionicus histrionicus

Britannique pour suivre leur acquisition de nutriments
femelles s'accroît de 7 % de la fin de l'hiver à la prémi-
ction du type de proies. Les femelles qui se nourrissent
ique (*Clupea pallasii* Valenciennes, 1847) deviennent
et elles semblent être plus lourdes que les femelles qui
stéropodes, durant la période fraye des harengs (mars). À
les masses corporelles semblables; alors que les oiseaux
aux sites avec fraye maintiennent leur gain de masse an-
x à ces différents sites ont des régimes alimentaires très
femelles visent une masse corporelle prémigratoire opti-
urabondante; cette masse corporelle s'explique sans doute
la migration et la reproduction.

Introduction

There is increasing recognition that cross-seasonal effects should be considered when investigating life-history strategies and trade-offs (Tamisier et al. 1995; Gates et al. 2001; Boos et al. 2002; Webster et al. 2002), including those related to nutrient acquisition and allocation. Individuals carry over effects on condition from one season to the next, and these residual effects can influence demographic attributes such as reproductive success and annual survival (Webster et al. 2002). This may be especially true for migratory birds that require considerable energy to move between wintering and breeding areas and successfully reproduce (Raveling and Heitmeyer 1989). Seasonal variation in nutrient acquisition

Jönsson 1997). Decisions on how to balance these costs and benefits are further influenced by the environment in which the species resides, where predictability and accessibility of exogenous food sources may reduce the need for endogenous stores (Jönsson 1997).

In waterfowl, strategies of nutrient acquisition for meeting costs of migration and reproduction differ spatially and temporally among species. For example, McLandress and Raveling (1981) found that Giant Canada Geese (*Branta canadensis maxima* L., 1758) undergo considerable fattening before they leave wintering sites, while Gauthier et al. (1992) determined that Greater Snow Geese (*Chen caerulescens atlantica* L., 1758) store nutrients while on spring staging areas. Other species such as Wood Ducks (*Aix sponsa* (L., 1758); Drobney 1982), Ruddy Ducks (*Oxyura jamaicensis* (J.F. Gmelin, 1789); Tome 1984), and Greater Scaup (*Aythya marila* (L., 1761); Gorman 2005) appear to store nutrients after arrival on nesting areas.

The extent to which Harlequin Ducks (*Histrionicus histrionicus* (L., 1758)) build and use endogenous stores for migration and reproduction is unknown. If Harlequin Ducks store endogenous reserves for migration and subsequent investment in reproduction, it is important to determine where and when they build these nutrient stores to understand their nutrient acquisition strategy and potential constraints to nutrient acquisition. Harlequin Ducks winter in marine environments and generally consume intertidal invertebrates such as snails, crabs, amphipods, and limpets. In spring, these ducks migrate to freshwater streams for nesting, where they consume freshwater invertebrates (Robertson and Goudie 1999). Pacific herring (*Clupea pallasii* Valenciennes, 1847) spawn is a key feature of the wintering habitat of Harlequin Ducks on the Pacific coast that could influence nutrient stores. For 3–4 weeks in late winter – early spring, herring roe is superabundant and some Harlequin Ducks are known to aggregate at herring spawning sites (Vermeer et al. 1997; Rodway et al. 2003). Rodway and Cooke (2002) determined that herring eggs are the principal prey for these aggregated ducks throughout the spawning period. The ecological implications of this food source have received little investigation, although there has been speculation about potential benefits to survival and (or) reproductive performance (Rodway et al. 2003; Žydelis and Esler 2005).

To investigate the timing of nutrient storage in Harlequin Ducks, as well as the mediating effects of forage type, we measured body mass of captured adult female Harlequin Ducks in winter prior to spring migration. Although mass-based measurements do not allow differentiation of body stores into various components, they do show changes in overall nutrient storage over time. Generally, lipids are considered the most efficient source of fuel for migration (Witter and Cuthill 1993; Jenni and Jenni-Eiermann 1998) and the most common nutrients stored for clutch formation uals that consume different food types. The heavy isotope of nitrogen (^{15}N) is preferentially incorporated into tissues of the consumer from the diet, which results in a systematic enrichment in the nitrogen stable isotope ratio with increases in trophic level (Kelly 2000). For this study, we

ods. There was more uncertainty surrounding mass dynamics during the midspawning period, although the high AIC_cW for models 1 and 2 combined (summed AIC_cW = 0.881) supports the conclusion that masses differed between sites during midspawning. Also, models in which midspawning data from both sites were combined, either lumped with postspawning data (model 4) or alone (model 5), were not well supported (AIC_cW of 0.045 and 0.015, respectively).

To summarize, our analysis provided support for the conclusions that body mass (after accounting for body size) of adult female Harlequin Ducks was similar between spawning and non-spawning sites prior to spawning, that females on spawning sites increased mass substantially during the midspawning period while those on non-spawning sites seemed to maintain their earlier mass, and that masses were similar between sites during the postspawning period owing to increases in mass of birds from non-spawning sites and maintenance of previously gained mass by birds from spawning sites. The change in average body mass (±SE) between prespawning and postspawning periods, for both sites, was 40 ± 10 g, an increase of 7% ± 1.8% (Fig. 2). Although sample size of females captured during midspawning on non-spawning sites was low, the data support the conclusion that the chronology of mass gain may depend on the prey consumed (i.e., herring roe or marine invertebrates), and this finding warrants further investigation.

Discussion

Like many waterfowl, adult female Harlequin Ducks store endogenous nutrients on wintering areas prior to spring migration. Our data indicate that despite dramatic differences in forage type and availability between herring spawning sites and non-spawning sites, females from both areas achieved a similar body mass prior to departure from wintergration (Žydelis and Esler 2005) may depend on this food source for breeding on potentially food-limited sites. The proportion of a population that aggregates on herring spawning sites may be indicative of the population's dependence on spawn for meeting energetic costs (Vermeer et al. 1997), as illustrated by the fact that not all Harlequin Ducks in the Strait of Georgia aggregated during spawning events. Elucidating strategies for meeting the demands of migration and reproduction, including the role of herring spawn, is critical for informed management and conservation of bird species. As well, these strategies highlight the importance of considering cross-seasonal effects when managing populations.

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