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Cross-seasonal dynamics in body mass of male Harlequin Ducks: a strategy for meeting costs of reproduction

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Abstract: Considerations of acquisition of energy for reproduction by waterfowl have disproportionately focused on females, although males also require energy for reproduction. We quantified variation in body mass of male Harlequin Ducks (*H* (L., 1758)) on coastal wintering areas prior to spring migration, as well as on breeding grounds, to determine when and where nutrients were acquired to meet costs of reproduction. Male mass on wintering grounds increased, on average, by 45 g (7%) in the weeks prior to migration. On breeding streams, we inferred that body mass of paired males decreased with the length of time on breeding grounds. Also, on average, male mass was considerably lower on breeding streams than when they departed coastal wintering sites. We conclude that males store nutrients on marine wintering grounds for subsequent use during the breeding season. Male Harlequin Ducks are highly vigilant while on breeding streams and the associated reduction in feeding time presumably requires energy stores. We suggest that males have evolved a strategy that is at least partially ‘‘capital’’ for meeting costs of reproduction, in which they acquire an optimal amount of energy reserves prior to spring migration and subsequently invest them in behaviours that can enhance reproductive success.

Résumé : Les discussions sur l’acquisition d’énergie pour la reproduction chez la sauvagine se sont intéressées de façon disproportionnée aux femelles, alors que les mâles ont aussi besoin d’énergie pour la reproduction. Nous mesurons la variation de la masse corporelle chez des arlequins plongeurs (*H*

standing how both males and females meet the costs of reproduction has important implications for understanding whether there are nutritional constraints on productivity, and when and where such constraints might be manifested. In turn, this understanding provides insight into opportunities for conservation activity to affect reproductive performance. Furthermore, there is growing appreciation for the importance of cross-seasonal, or carry-over, effects between stages of the annual cycle (Esler 2000; Webster et al. 2002; Norris 2005; Norris and Taylor 2006).

Studies of female waterfowl reproductive energetics demonstrate that there can be considerable interspecific variation in strategies of when and where nutrients and energy for reproduction are acquired. Females of some species generally build reserves prior to arrival on breeding areas, either on wintering or spring staging sites, and subsequently invest both the wintering and breeding data sets. Captured males were banded, weighed, and measured (exposed culmen length, diagonal tarsal length, flattened wing chord), and their pair status was recorded. Capture dates on breeding streams corresponded to prelaying and laying periods for most pairs.

On breeding streams, lipid biopsies were taken from all captured females, following methods described in detail by Bond et al. (2007). We used the carbon stable isotope ratios of these biopsies to estimate the amount of time that the associated paired male had been on the breeding stream. Because ( ) stable isotopes are incorporated into the tissues of animals through their diet, ( ) freshwater environments have a much more depleted stable isotope signature than marine environments, and ( ) stable isotope ratios turn over in tissues as the consumer switches diets (Tieszen et al. 1983; Hobson and Clark 1992; 1993), we were able to infer the relative lengths of time that males had been on breeding streams (Phillips and Eldridge 2006). In other words, males with partners that had more enriched (i.e., more marine) carbon isotope signatures were presumed to be more recent arrivals on the breeding grounds. Harlequin Ducks are known to pair on the wintering grounds and migrate to breeding areas together (Robertson et al. 1998). Stable isotope laboratory methods are detailed in Bond et al. (2007); isotope values are expressed in delta notation ($\delta^{13}C$), which is a ratio of the heavier to lighter isotope relative to a standard in parts per thousand.

Sta t t ca a a 9

For wintering birds, we used general linear models to evaluate variation in body mass of after-hatch-year male Harlequin Ducks (= 182) on marine areas in relation to spawn site status (spawning or nonspawning) and period (prespawning, midspawning, or postspawning). We employed information–theoretic methods to direct model selec-
ease-

Tab 9 1. Candidate models describing variation in body mass of male Harlequin Ducks (*H* -
) on wintering grounds prior to spring migration in relation to period and site status, where periods consist of before herring spawn (pre), during herring spawn (mid), and following herring spawn (post), and site status refers to herring spawn sites (S) and nonspawn sites (N).

Model rank	Structure of candidate models	*K**	AIC_c†	ΔAIC_c‡	§

reserves on marine wintering sites that were subsequently used to meet costs of reproduction that they incurred on breeding streams. We found that body mass of adult male Harlequin Ducks on wintering areas increased by ~45 g between late winter and departure for spring migration. When captured on breeding streams, mean body mass had declined to a level similar to that on wintering areas prior to the late-winter mass gain described above. Some of that mass loss higher on spawn sites (Fig. 1); however, this does not change the conclusion that mass was similar between sites by the end of winter. Because herring spawn is not required for nutrient acquisition, there may be other reasons, such as social interaction or reduced predation, that explain why Harlequin Ducks aggregate at herring spawn sites (Rodway et al. 2003; Žydelis and Esler 2005; Bond and Esler 2006).

Energetic and nutritional costs of reproduction have been more thoroughly investigated in female anatids, but males also may be constrained in their abilities to meet energetic requirements during the breeding season (Choinière and Gauthier 1995; Hipes and Hepp 1995). Similar to our findings for male Harlequin Ducks, male Wood Ducks (*A* (L., 1758)) showed a decline in body mass during the breeding season, which was attributed to vigilance and mate guarding (Hipes and Hepp 1995). Also, Choinière and Gauthier (1995) found that male Greater Snow Geese (*C* Kennard, 1927) had declining nutrient reserves prior to incubation and that the reduction of body reserves was more severe in males than in females. Our data show that male and female Harlequin Ducks use somewhat different strategies for meeting costs of reproduction. Males have at least a partial capital strategy, whereas females use an income strategy to meet egg production costs (Bond et al. 2007), although they likely invest reserves built on wintering sites during later reproductive stages.

A growing body of literature suggests that nutritional status of male waterfowl, like females, could have important effects on reproductive success and population-level productivity. For example, deterioration of habitat conditions on the wintering grounds could influence male nutrient acquisition prior to breeding, which in turn could carry over to the breeding grounds and affect female breeding success and survival through decreases in male vigilance. These types of cross-seasonal effects are increasingly appreciated as complex but important issues to address for understanding population dynamics of migratory animals (Esler 2000; Webster et al. 2002; Norris 2005; Norris and Taylor 2006).

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