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 (*Histrionicus histrionicus* (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 (*Histrionicus histrionicus* (L., 1758)) dans des zones côtières d'hivernage avant la migration printanière, ainsi que sur les lieux de reproduction, afin de déterminer quand et où ils acquièrent les nutriments nécessaires pour combler les coûts de leur reproduction. Sur les zones d'hivernage, la masse des mâles augmente en moyenne de 45 g (7 %) dans les semaines qui précèdent la migration. Dans les cours d'eau de reproduction, nous supposons que la masse corporelle des mâles appariés diminue en fonction du temps passé sur les aires de reproduction. De plus, en moyenne, la masse des mâles dans les cours d'eau de reproduction est considérablement réduite par rapport à leur masse au départ des zones côtières d'hivernage. Nous concluons que les mâles stockent des nutriments sur les zones marines d'hivernage pour utilisation subséquente durant la saison de reproduction. Les arlequins plongeurs mâles sont très vigilants durant leur séjour dans les cours d'eau de reproduction et la réduction de la période alimentaire qui en résulte nécessite sans doute des réserves alimentaires. Nous croyons que les mâles ont développé une stratégie qui est au moins en partie « capital » pour combler les coûts de leur reproduction, dans laquelle ils acquièrent une quantité optimale de réserves énergétiques avant la migration printanière et les investissent ensuite dans des comportements qui peuvent accroître leur succès reproductif.

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Introduction

Considerable research effort has been devoted to understanding strategies by which female waterfowl meet the energetic and nutritional costs of reproduction, particularly egg production (Alisauskas and Ankney 1992; Esler et al. 2001;

Bêty et al. 2003; Gauthier et al. 2003). While costs of reproduction to male waterfowl are acknowledged or implied (Gauthier and Tardif 1991; Mann and Sedinger 1993; Christensen 2000; Guillemain et al. 2003; Squires et al. 2007), quantifying these costs and determining how they are met has received much less attention than for females. Under-

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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 those reserves in clutch formation (Parker and Holm 1990) or during subsequent reproductive stages (Bond and Esler 2006). Such strategies have been referred to as "capital" breeding (Jönsson and Jonsson 1997). A variation of a capital strategy occurs when females arrive on breeding areas and build reserves prior to reproduction and subsequently invest those reserves in the reproduction (Esler et al. 2001). Alternatively, some species pay costs of reproduction directly via food consumption on breeding areas, termed an "income" strategy (Mann and Sedinger 1993; MacCluskie and Sedinger 2000; Gorman et al. 2008). It is increasingly appreciated that the capital–income relationship is not a dichotomy, but a continuum (Jönsson and Jonsson 1997), with many species falling somewhere between the extremes, using both stored reserves and available food to fund reproductive effort.

Male waterfowl presumably adopt various strategies throughout the capital–income continuum for meeting the reproductive costs that they incur. We evaluated variation in body mass of male Harlequin Ducks (*Histrionicus histrionicus* (L., 1758)) in southern British Columbia from late winter through breeding to consider their use of nutrient reserves to meet the energetic costs of reproduction. Male Harlequin Ducks demonstrate a high degree of vigilance on breeding streams, with correspondingly low rates of feeding (Inglis et al. 1989; Rodway 1998; Goudie and Jones 2005; Squires et al. 2007). Because males do not assist in incubation or brood-rearing, and leave breeding streams shortly after the female begins incubation, we suggest that mate guarding and vigilance are the primary reproductive costs for males. There are several hypothesized benefits of vigilance (Squires et al. 2007), and presumably there are associated energetic costs that must be met. Vigilance may limit the males' ability to acquire food resources while on the breeding grounds, and therefore, it is plausible that they would store nutrients prior to the breeding period.

In this paper, we document changes in body mass from late winter to departure for spring migration on marine wintering areas and on the breeding grounds prior to female incubation to determine if males were building reserves on nonbreeding habitat that subsequently were used during the breeding season. An important feature of the wintering areas of Harlequin Ducks on the west coast of North America is the occurrence of Pacific herring (*Clupea pallasii* Valenciennes, 1847) spawn just prior to spring migration. Harlequin Ducks are known to aggregate to feed on this super abundant food resource (Rodway et al. 2003), but the energetic importance of this has only been recently considered, specifically for females (Bond and Esler 2006). We captured male Harlequin Ducks in both herring spawning and nonspawning sites to consider the importance of herring spawn for nutrient acquisition in this sex.

Our specific questions were (*i*) do male Harlequin Ducks build nutrient reserves and subsequently use them during the reproductive period on breeding areas; (*ii*) when and where are these reserves acquired; and (*iii*) do dynamics in body mass differ between individuals that forage on herring spawn and those that do not.

Materials and methods

Collection of field data

We captured Harlequin Ducks on wintering areas in the Strait of Georgia, British Columbia, using a floating mist-net capture method modified for inshore use (Kaiser et al. 1995). Captured birds were immediately removed from the net, and then banded and weighed on an electronic balance (±1 g). Males were identified as hatch year (i.e., hatched the previous summer) or after-hatch year based on plumage (Smith et al. 1998). We conducted captures at sites both with and without herring spawn during three periods in 2004: prespawning (27 February – 5 March), midspawning (19–27 March), and postspawning (2–11 April). The postspawning period preceded the departure of nearly all Harlequin Ducks from wintering areas. Capture locations were determined based on historical records of herring spawn occurrence (Fisheries and Oceans Canada 2004). Herring spawn is a conspicuous event, and thus the categorization of sites and periods into those with and without spawn is definite. Capture sites with spawn included locations around Hornby Island (49°31′N, 124°42′W), Denman Island (49°32′N, 124°49′W), and Qualicum Bay (49°24′N, 124°38′W), while nonspawn capture sites included locations around southeast Quadra Island (50°12′N, 129°15′W) and Williams Beach (49°52′N, 125°07′W). Harlequin Ducks from our nonspawn capture sites had been previously determined (Rodway et al. 2003) to be unlikely to move to herring spawn sites, and stable isotope analyses of females confirmed this (Bond and Esler 2006); we assume that this holds true for males as well.

On the breeding grounds, we captured Harlequin Ducks using mist nets set up in streams from 9 to 20 May 2003 and from 21 April to 20 May 2004, in the southern Coast Mountains of British Columbia, Canada. The study area was near the towns of Pemberton (50°19′N, 122°48′W) and Lillooet (50°41′N, 121°56′W), and included the following streams: Bridge River, Seton River, Cayoosh Creek, Yalakom River, Ryan River, Rutherford Creek, and Brandywine Creek. Distances between wintering and breeding study sites were between 200 and 250 km. Extensive mark–resight data have demonstrated that Harlequin Ducks migrate directly inland from the Strait of Georgia and there are several records of marked individuals being sighted both on the breeding streams we studied and in the coastal areas where wintering work was conducted (C. Smith, unpublished data). However, none of the individuals in our analyses were represented in

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 (*i*) stable isotopes are incorporated into the tissues of animals through their diet, (*ii*) freshwater environments have a much more depleted stable isotope signature than marine environments, and (*iii*) 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.

Statistical analyses

For wintering birds, we used general linear models to evaluate variation in body mass of after-hatch-year male Harlequin Ducks ($n = 182$) 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 selection (Burnham and Anderson 2002). The set of candidate models included biologically plausible ways of grouping body mass data by site status and period combinations (Table 1). We determined the sum of squared errors for each model and calculated Akaike's information criterion for small sample sizes (AIC_c; Table 1), which indicates the degree of parsimony of each model given the data and set of models considered. We also calculated the differences between these values for each model in relation to the best-fitting model (ΔAIC_c) and the AIC_c weights (w_i) for each model, which convey the relative support for each model in the candidate model set.

To evaluate male body mass on the breeding grounds relative to wintering grounds ($n = 229$), we created a new set of candidate models. Starting with the best-supported model from the winter analysis, we created several models representing different groupings, in which breeding ground body mass was included with different wintering groups or treated as a separate group (Table 2). We again used information–theoretic methods, as described above, to direct our model selection. Body mass data from both breeding seasons were combined, as means (±SE) were similar between years (632 ± 7 g in 2003 and 618 ± 8 g in 2004).

We used an information–theoretic approach to evaluate the relationship between abdominal lipid $\delta^{13}C$ signatures of

females (as a proxy for time since arrival) and body mass of the paired males on breeding grounds. Our sample size reflects those birds for which both members of the pair were captured and the female's abdominal lipid analyzed ($n = 15$). We recorded measurements of body size for males captured on breeding streams, and thus were able to include a principal component score in our candidate set of models to consider the effects of body size on body mass (Table 3). The PC_1 score was positively related to the morphometric measurements included (tarsus, culmen, and wing chord) and had an eigenvalue of 1.27, explaining 43% of the original variance. Least-squares general linear models were used for this analysis including all additive combinations of female lipid isotope ratio and PC_1 score, as well as a null model (Table 3). All data sets met underlying assumptions of least-squares general linear models.

Results

Mean body mass of male Harlequin Ducks steadily increased from late winter to spring migration and did not differ markedly based on herring spawn status (Fig. 1). The best supported model ($w_i = 0.219$; Table 1) described changes in body mass by period but not by spawn status. However, there was modest support (models 2–8; Table 1) for competing models that described various groupings in the prespawning and midspawning periods, suggesting some differences by spawn status. In particular, there was some indication that males on spawn areas during prespawning had lower masses than those on nonspawn areas and also that the differences in mass between prespawning and midspawning was greater for birds consuming spawn than those that did not. Despite that uncertainty, the analysis was very clear that during the postspawning period, just prior to migration, males from both spawn and nonspawn sites had similar body masses and that these masses were higher than at least some earlier periods (summed $w_i = 0.98$). The mean (±SE) increase in body mass between prespawning and postspawning periods was 45 ± 7.8 g ($7.2\% \pm 1.3\%$; Fig. 1).

The mean male body mass on breeding grounds was similar to the mean body mass of males captured during the prespawning period, and distinctly lower than the mean body mass on wintering areas just prior to migration (Table 2, Fig. 1). The model describing this pattern was strongly supported with $w_i = 0.735$.

Male body mass on breeding areas was related to the lipid stable isotope signatures of their female mates ($w_i = 0.508$; Table 3). Male body mass declined with decreasing $\delta^{13}C$ values (Fig. 2), suggestive that mass was lower for those males that had been on the breeding grounds longer. The model equation (with SE in parentheses following parameter estimates) was male body mass = 753.2 (42.6) + 5.1 (1.7) × $\delta^{13}C$ female lipid ($R^2 = 0.40$). The next best-supported model, with $w_i = 0.388$, described a similar relationship after accounting for body size. The model with PC_1 score only was ranked below the null model, indicating that body size by itself did not explain important variation in male body mass.

Discussion

Adult male Harlequin Ducks employed at least a partial capital strategy of nutrient acquisition, in which they built

Table 1. Candidate models describing variation in body mass of male Harlequin Ducks (*Histrionicus histrionicus*) 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).

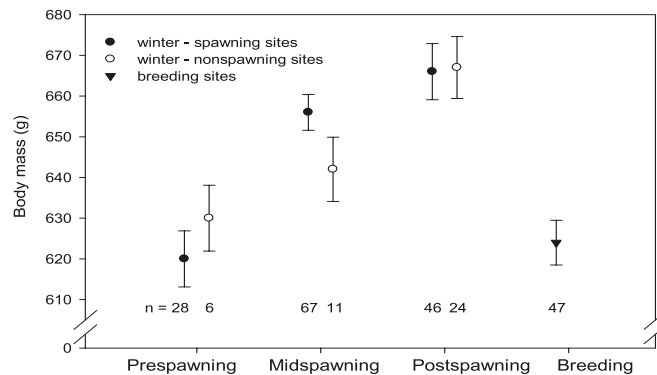| Model rank	Structure of candidate models	K*	AIC_c[†]	ΔAIC_c[‡]	w_i[§]
1	preN = preS, midN = midS, postN = postS	4	1333.3	0.000	0.219
2	preS, preN = midN, midS, postN = postS	5	1334.2	0.950	0.136
3	preN = preS = midN, midS, postS = postN	4	1334.3	0.989	0.134
4	preS, preN = midN, midS = postN = postS	4	1334.9	1.647	0.096
5	preN = preS = midN, midS = postS = postN	3	1335.0	1.677	0.095
6	preN, preS, midN = midS, postN = postS	5	1335.1	1.813	0.089
7	preS, preS = midN = midS, postS = postN	4	1335.2	1.880	0.086
8	preN = preS, midN = midS = postN = postS	3	1335.4	2.075	0.078
9	preN, preS, midN = midS = postN = postS	4	1337.2	3.871	0.032
10	preN, preS, midN, midS, postN, posts	7	1338.2	4.863	0.019
11	preS, preS = midN = midS = postN = postS	3	1338.5	5.243	0.016
12	preN = preS = midN = postN, midS = postS	3	1350.5	17.19	0.000
13	preN = preS = midS = midN = postS = postN	2	1358.1	24.76	0.000
14	preN = preS = midN = postS = postN, midS	3	1359.6	26.30	0.000
15	preN = midN = postN, preS = midS = postS	3	1360.0	26.71	0.000

*K is the number of parameters estimated in the model.
[†]AIC_c is Akaike's information criterion corrected for small sample sizes.
[‡]ΔAIC_c is the difference in AIC_c relative to the best-fitting model.
[§]w_i is the AIC_c weight or model likelihood.

Table 2. Candidate models describing variation in body mass of male Harlequin Ducks (*Histrionicus histrionicus*) on breeding grounds in relation to the best model (model 1; Table 1) describing wintering body mass, where periods consist of before herring spawn (pre), during herring spawn (mid), following herring spawn (post) and on the breeding grounds (breed).

Model rank	Structure of candidate models	K*	AIC_c[†]	ΔAIC_c[‡]	w_i[§]
1	pre = breed, mid, post	4	1672.0	0.000	0.735
2	pre, mid, post, breed	5	1674.0	2.039	0.265
3	pre, mid = breed, post	4	1689.6	17.39	0.000
4	pre, mid, post = breed	4	1705.1	33.11	0.000
5	pre = mid = post = breed	2	1715.8	43.85	0.000

*K is the number of parameters estimated in the model.
[†]AIC_c is Akaike's information criterion corrected for small sample sizes.
[‡]ΔAIC_c is the difference in AIC_c relative to the best-fitting model.
[§]w_i is the AIC_c weight or model likelihood.

Table 3. Candidate models describing variation in body mass of male Harlequin Ducks (*Histrionicus histrionicus*) on breeding grounds in relation to the stable isotope signatures of paired female abdominal lipid; in the model description, lipid refers to the carbon stable isotope signature of abdominal lipid in the male's paired female and PC_1 is the principal component score, which accounts for body size.

Model rank	Structure of candidate models	K[a]	AIC_c[†]	ΔAIC_c[‡]	w_i[§]
1	Lipid	3	105.6	0.000	0.508
2	Lipid + PC_1	4	106.1	0.538	0.388
3	Null	2	110.1	4.524	0.053
4	PC_1	3	110.2	4.576	0.052

[a]K is the number of parameters estimated in the model.
[†]AIC_c is Akaike's information criterion corrected for small sample sizes.
[‡]ΔAIC_c is the difference in AIC_c relative to the best-fitting model.
[§]w_i is the AIC_c weight or model likelihood.

Fig. 1. Dynamics in body mass (mean ± SE) of adult male Harlequin Ducks (*Histrionicus histrionicus*) on wintering and breeding sites. Wintering birds are categorized by period (prespawning, midspawning, postspawning) and Pacific herring (*Clupea pallasii*) spawn status (spawn and nonspawn).

Fig. 2. Change in body mass of male Harlequin Ducks (*Histrionicus histrionicus*) in relation to carbon (δ^{13}C) stable isotope signatures of paired female abdominal lipid, which is assumed to be an index to the amount of time males had been on breeding streams.

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 could have occurred during migration; however, Harlequin Ducks are short-distance migrants, with a mean distance between our wintering and breeding study sites of 235 km, and estimates of flight costs of females (Bond 2005) indicate that this could account for only a small portion of observed changes in body mass. In addition, our analysis including female isotope ratios suggested that male mass declined as a function of the amount of time they had been on breeding streams, with the estimated mass at arrival (Fig. 2) very similar to that just prior to departure from wintering areas (Fig. 1). Taken together, these results strongly indicate a strategy in which males build nutrient reserves on coastal sites and allocate those to reproduction while on inland streams. If males were employing an income strategy, we would not expect to detect observed increases in mass on wintering areas, the large difference between mean masses of males prior to departure of coastal areas and those on breeding areas, nor declines in body mass associated with estimates of time on breeding streams. Also, a completely capital strategy would imply that males would not feed at all while guarding their mate, which is known to be untrue (Rodway 1998; Squires et al. 2007). Therefore, our data indicate that male Harlequin Ducks employ a partial capital strategy of nutrient acquisition and allocation in support of reproduction.

We suggest that the nutrient acquisition strategy of male Harlequin Ducks has evolved to meet energetic costs of vigilance and mate guarding. Male Harlequin Ducks spend only about 17% of their time feeding while on breeding streams (Rodway 1998) and spend more time vigilant when females are feeding, especially in locations where they may be more susceptible to predation (Squires et al. 2007). There are distinct fitness advantages associated with vigilance and mate guarding. Males can use vigilance to ensure paternity, as
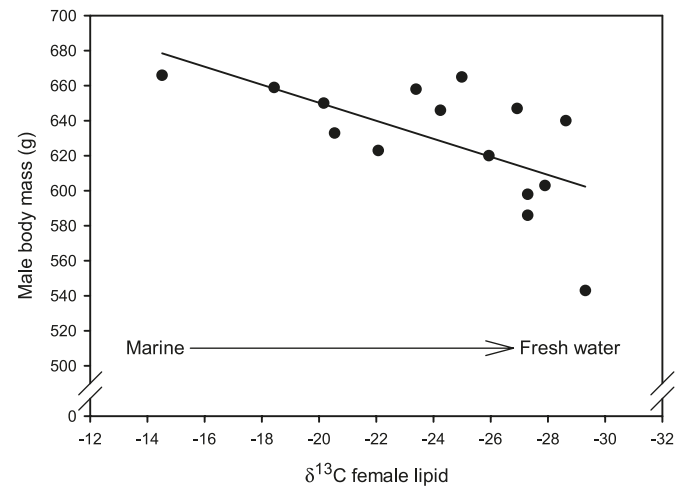
well as survival of self or partner (Christensen 2000; Guillemain et al. 2003). In a recent study of Harlequin Ducks, Squires et al. (2007) concluded that their data supported the male vigilance for female benefit hypothesis through increased female survival. Male vigilance may also increase female breeding success by allowing females to feed to meet costs of egg production, which have been demonstrated to be met with nutrients acquired by the female on breeding streams (Bond et al. 2007). Therefore, a high degree of vigilance can result in increased reproductive success, and may have benefits beyond the current breeding season given evidence of long-term pair bonds in Harlequin Ducks (Robertson et al. 1998) and associated benefits that can be realized only if the female survives. Because there is a trade-off between vigilance and time spent feeding (Squires et al. 2007), there is a clear selective advantage to males to carrying and using reserves acquired prior to arrival on breeding streams.

We found that male body mass increased on wintering sites regardless of whether or not they fed on superabundant herring roe. Female Harlequin Ducks also build reserves on wintering areas and, like males, achieve a similar body mass irrespective of herring spawn consumption (Bond and Esler 2006). In the case of females, individuals on nonspawn sites were confirmed, via stable isotope analysis, to have not consumed herring spawn and we assume that this is also true of males captured at nonspawn sites. Our results suggest that male Harlequin Ducks, like females (Bond and Esler 2006), do not require herring spawn to build premigratory nutrient reserves. It further suggests that there is an optimal departure body mass for males, which balances the costs and benefits of nutrient acquisition, that is less than the maximum possible, given that males on herring spawn sites could forage much more intensively than they do (Rodway and Cooke 2001). Consumption of herring spawn by female Harlequin Ducks was shown to change the timing of premigratory mass gain, with individuals on spawn sites gaining mass earlier (Bond and Esler 2006). Our data for males hint at this too, with mass during midspawn averaging somewhat

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 (*Aix sponsa* (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 (*Chen caerulescens atlantica* 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).

Acknowledgements

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