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Source: The Auk, 124(1) : 241-252

Published By: American Ornithological Society

URL: [https://doi.org/10.1642/0004-8038\(2007\)124\[241:VBITHD\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2007)124[241:VBITHD]2.0.CO;2)

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VIGILANCE BEHAVIOR IN THE HARLEQUIN DUCK (*HISTRIONICUS HISTRIONICUS*) DURING THE PREINCUBATION PERIOD IN LABRADOR: ARE MALES VIGILANT FOR SELF OR SOCIAL PARTNER?

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ABSTRACT.—Males of several avian species are more vigilant than their female partners, particularly during the preincubation period. Male vigilance may function as a deterrent of extrapair copulation attempts (EPCs) or to ensure male survival, because males of sexually dimorphic species may be more conspicuous to predators than females. However, vigilant males may act as antipredator sentinels to enhance female survivorship, which may also allow females to feed and rest more efficiently, thereby enhancing their ability to form clutches. We attempted to distinguish between the “male benefits” and “female benefits” hypotheses by studying the behavior of unpaired males and paired Harlequin Ducks (*Histrionicus histrionicus*) during the preincubation period. Paired males were, on average, four times more vigilant than unpaired males and their mates, which suggests that elevated levels of vigilance by paired males does not function primarily for self-protection against predators. Males were not more vigilant during the female's fertile period, contrary to the “paternity assurance” hypothesis. Male vigilance during feeding bouts was highest when pairs fed alone near shore—a condition in which feeding was likely more “risky.” Male vigilance was positively correlated with female feeding when females fed near shore, but not at other times. During resting bouts, males were vigilant $14 \pm 0.01\%$ of the time in all conditions. We suggest that male vigilance may be important to enhance female survival, especially when females feed under risky conditions. Received 9 December 2004, accepted 15 February 2006.

Key words: Harlequin Duck, *Histrionicus histrionicus*, male investment, mate-guarding, predation risk, preincubation, vigilance.

Comportement de Vigilance chez *Histrionicus histrionicus* durant la Période de Pré-incubation au Labrador: Les Mâles Sont-ils Vigilants pour Eux-mêmes ou pour leur Partenaire Social?

RÉSUMÉ.—Les mâles de plusieurs espèces aviaires sont plus vigilants que leur partenaire femelle, particulièrement durant la période de pré-incubation. La vigilance des mâles peut fonctionner comme un moyen de dissuasion contre les tentatives de copulation extra-conjugale (CEC) ou pour assurer la survie du mâle, car les mâles des espèces affichant un dimorphisme sexuel peuvent être plus faciles à repérer par les prédateurs que les femelles. Néanmoins, les mâles vigilants peuvent agir comme des sentinelles anti-prédateur pour augmenter la survie des

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femelles, ce qui peut aussi permettre aux femelles de se nourrir et se reposer plus efficacement, et ainsi augmenter leur aptitude à produire des œufs. Nous avons tenté de distinguer les hypothèses de « bénéfice au mâle » et « bénéfice à la femelle » en étudiant le comportement des mâles non appariés et des couples d'Arlequins plongeurs (*Histrionicus histrionicus*) durant la période de pré-incubation. Les mâles appariés étaient, en moyenne, quatre fois plus vigilants que leur femelle et les mâles non appariés, ce qui suggère que les niveaux élevés de vigilance des mâles appariés n'ont pas essentiellement pour fonction leur propre protection contre les prédateurs. Les mâles n'étaient pas plus vigilants au cours de la période fertile de la femelle, contrairement à l'hypothèse « d'assurance de la paternité ». La vigilance des mâles durant les épisodes d'alimentation était plus élevée lorsque les couples s'alimentaient seuls près de la rive – une condition pour laquelle l'alimentation était apparemment plus « risquée ». La vigilance des mâles était positivement corrélée avec l'alimentation de la femelle seulement lorsque les femelles s'alimentaient près de la rive. Lors des épisodes de repos, les mâles étaient vigilants $14 \pm 0.01\%$ du temps dans toutes les conditions. Nous suggérons que la vigilance du mâle peut être importante pour accroître la survie de la femelle, spécialement lorsque les femelles s'alimentaient dans des conditions risquées.

SEVERAL STUDIES HAVE found that male birds are more vigilant than their female partners during the preincubation period (e.g., Gauthier and Tardif 1991, Hannon and Martin 1992, Artiss and Martin 1995). Typically, male vigilance is assumed to benefit males, ensuring either their survival or paternity. Higher vigilance may be characteristic of brightly colored male birds, because they may be more susceptible to predation (Huhta et al. 2003). The "male survival" hypothesis predicts similar vigilance levels between unpaired and paired males in breeding plumage. The "paternity assurance" hypothesis proposes that males use vigilance as a mate-guarding strategy to prevent being "cuckolded" by extrapair copulations (EPCs) by other males (Brodsky 1988, Guillemain et al. 2003). Vigilance may be used to survey surroundings for potential EPC attempts or may serve as a behavioral signal to deter other males. Under this hypothesis, males should be more vigilant in the presence of conspecific males, especially when females are laying eggs, a time when EPCs are most likely to result in fertilization (Birkhead 1998).

There is growing consensus that females exert considerable control over paternity, and alternative functions have been proposed for behaviors traditionally associated with paternity assurance (Stamps 1997, Stutchbury and Neudorf 1997). Alternative functions appear to be plausible, given that selection should favor male behaviors that enable their female

partners to increase their reproductive success. There is evidence that females of some species choose vigilant males, which suggests that male vigilance is important to females (Dahlgren 1990, Choudhury and Black 1993, Pizzari 2003). The "female benefits" hypothesis proposes that males use vigilance behaviors in predator detection to enhance female survival and to allow females more foraging and resting time to enhance their nutritional status (Lamprecht 1989, Artiss and Martin 1995, Black et al. 1996, Artiss et al. 1999, Black 2001). Males may be vigilant for predators to enhance female survival without a subsequent effect on female feeding and resting. The "female survival" hypothesis predicts higher male vigilance under conditions that confer higher predation risk, such as when pairs are alone and unable to benefit from group vigilance. Alternatively, male vigilance for predators may allow females more time to feed and rest, either as a direct investment by males, or because females capitalize on male vigilance for predators. In this scenario, there should be a positive correlation between the frequency of male vigilance and female behaviors such as feeding and resting. If nutritional status and reproductive performance are positively related, male vigilance should improve female reproductive output.

Benefits to paired females such as enhanced nutritional status and survival are often assumed to be byproducts of male attempts to

ensure paternity or their own survival (Artiss and Martin 1995, Artiss et al. 1999, Guillemain et al. 2003). Of the few studies testing for alternative functions of mate-guarding, most have focused on male aggression, not vigilance (e.g., Ashcroft 1976, Teunissen et al. 1985, Gauthier 1987, Christensen 2000). Few studies have attempted to distinguish between the “female benefits” and “male benefits” hypotheses to explain the function of male vigilance.

We studied the preincubation behavior of the Harlequin Duck (*Histrionicus histrionicus*), because the species is an ideal candidate for testing alternative hypotheses that explain male vigilance. Male investment in female nutritional status may be especially important in species in which breeding females face high-energy demands over a short period. For precocial species like the Harlequin Duck, energetic requirements for breeding are highest and most limiting to reproductive success during the preincubation period (Alisauskas and Ankney 1992, Carey 1996). This is especially true for “income-breeding” species like the Harlequin Duck, in which females form clutches from nutrients acquired on breeding sites during the preincubation period, rather than from nutrient reserves acquired from wintering areas (Jönsson 1997, Bond 2005). Previous studies on the Harlequin Duck have found that males spent 16% less time feeding than females during winter (Torres et al. 2002), and 20–30% less time feeding during the preincubation period (Bengston 1972, Hunt 1998, Rodway 1998). Additional study is needed to determine whether males use time engaged in behavior different from their mates for themselves or as an investment in female nutritional status or survival.

Both members of a pair “mate-guard” by signaling with the “head-nod” display while positioning themselves between their mate and sexual competitors (Lazarus et al. 2004). Whether Harlequin Ducks use higher-level aggression to mate-guard is uncertain, because there have been no tests for alternative functions of higher-level aggression, such as defense of feeding and resting areas. However, Harlequin Ducks were aggressive <3% of the time in the present study (Squires 2003), and <6% of the time during studies in Iceland (Inglis et al. 1989, 2000). Given the relative rarity of aggression in this species, it is likely that males use behaviors other than aggression to ensure paternity. Thus,

we did not test for the function of aggression in the present study. Here, we use the proportion of time that Harlequin Ducks were vigilant (from time-activity data) to distinguish among hypotheses for the function of male vigilance. Paired males may be vigilant for all these reasons. However, each hypothesis generates testable predictions that can be used to distinguish them (summarized in Table 1).

METHODS

The study was conducted from May to July 2000 and 2001 at Fig Lake (53°03'N, 63°09'W) and from May to July 2001 at Nipishish Lake (54°02'N, 60°15'W) in Labrador, Canada. During the preincubation period, we captured Harlequin Ducks in mist nets and marked individuals with one metal and one colored tarsal band with a unique alphanumeric code. Observation periods were 30 min, using a focal, instantaneous sampling technique with a 15-s interval (Martin and Bateson 1986). We used date of clutch initiation as a measure of reproductive output and assumed that early-laying females were more productive. To determine date of clutch initiation, radiotransmitters (Holohil Systems, Carp, Ontario; 5–8 g, ~2% body mass) were mounted dorsally on seven adult females during the preincubation period using the anchor suture method (Pietz et al. 1995). For females without radiotransmitters, we estimated the date of clutch initiation to be 11 days before the start of incubation (Robertson and Goudie 1999). Onset of incubation was estimated as one day before the first day that paired males were consistently observed without the female. A period of higher female fertility was defined as two days before the start of clutch initiation to the start of incubation (hereafter “fertile period”). For observations collected at the Fig Lake site, the presence of other birds within sight of the focal pair was noted during observation sessions to determine whether the presence of conspecifics affected levels of paired male vigilance. Quantification of the number of nearby conspecifics (maximum six) was facilitated by the highly gregarious behavior of Harlequin Ducks. When pairs were observed with other birds, individuals were most often observed feeding and resting within ~5 m. Feeding bouts were defined by repeated dive cycles, and resting bouts were defined by

TABLE 1. Predictions and results used to distinguish between “male benefits” and “female benefits” hypotheses to explain the function of vigilance by male Harlequin Ducks during the preincubation period.

Hypothesis	Prediction	Results
Male survival	No difference in frequency of vigilance between unpaired males and paired males	Paired males were 4× more vigilant than unpaired males
Paternity assurance	Higher frequency of vigilance in paired males when females are most fertile	No difference between pre-fertile and fertile periods
	Higher frequency of vigilance in paired males in the presence of conspecifics	Small increase in paired male vigilance ($6 \pm 0.01\%$) in presence of conspecifics during resting
Female nutritional status	Positive correlation between frequency of male vigilance and female feeding and resting	Significant positive correlation between mean male vigilance and female feeding in lake habitat only
	Negative correlation between frequency of male vigilance and date of clutch initiation	No correlation
Female survival	Higher frequency of vigilance in paired males under risky conditions	Paired males were most vigilant when pairs fed in lake habitat in absence of conspecifics

the presence of individuals out of the water. Bouts of vigilance behavior were defined by side-to-side head scanning, sometimes with the neck extended upward, while on the surface between feeding (diving) bouts, or while out of the water during resting bouts.

In the Fig Lake site, we observed Harlequin Ducks in two habitat types distinguished by relative water speed. Harlequin Ducks were observed feeding and resting in the middle of fast-moving watercourses, typical habitat for this species (“stream”). We also observed Harlequin Ducks feeding and resting in slow-moving water, generally in small coves and bays (“lake”). Harlequin Ducks were generally observed resting the same distance from shore (approximately 5–10 m) in both fast- and slow-moving water. However, unlike in the more typical habitat, feeding in small coves and bays generally occurred <2 m from vegetation-lined lakeshores. We observed interactions between Harlequin Ducks and terrestrial predators, which suggests that areas of slow-moving water close to shore may be “risky” (Squires 2003). Over three years (1999–2001), Harlequin Ducks were observed to react on 16 occasions to the presence of ground predators (terrestrial and

aquatic), but only on 5 occasions to the presence of aerial predators (K. A. Squires unpubl. data). Because Harlequin Ducks drift in fast-moving water to escape predators (Robertson and Goudie 1999), nearshore, slow-moving water may be more risky habitat, because slow-moving water does not provide an escape mechanism and because terrestrial predators may be undetected in the dense riparian vegetation. Alternatively, slow-moving, nearshore water may be areas of lower predation risk, because female Harlequin Ducks sometimes conceal broods under overhanging vegetation when disturbed (Robertson and Goudie 1999). However, Harlequin Ducks were never observed as close to shore at any other times, such as when resting (K. A. Squires unpubl. data). The use of nearshore areas by disturbed brooding females may represent a trade-off between immediate risk and the potential risk posed by proximity to shore. Here, pairs fed along lakeshores where vegetation was dense but not overhanging and, thus, provided little cover. Feeding in such areas may pose added risk, because Harlequin Ducks may be less able to detect predators when diving underwater. We assumed that feeding in slow-moving water in proximity to shore was

a condition that conferred higher predation risk than feeding in midstream, fast-moving water. We also assumed that resting was more risky in small coves and bays because slow-moving water does not provide as effective an escape mechanism as fast-moving water.

To test the female survival hypothesis, we determined whether there were differences in the frequency of male vigilance between these two habitat types. To calculate overall means, we pooled data for the two males and six females for which we had two years of behavior data, because the mean proportion of time spent in behaviors differed between years by less than one standard error of the mean (<1 SE). To test the prediction of the "female nutritional status" hypothesis that females paired to vigilant males had higher reproductive success, we used Spearman's rank correlation to determine whether there was a negative correlation between the mean proportion of time spent vigilant by males and the date that females initiated clutches. Under this prediction, we assumed that early clutch initiation was an indicator of higher reproductive performance. To test the prediction of a positive correlation between male vigilance and female feeding and resting, we used means of observations for each individual as data points in Spearman's rank correlation analyses. To avoid pseudoreplication in correlation analyses, we used one year of data to calculate means for four females paired with different mates between years. We pooled data for two females paired to the same mate between years, because behaviors differed between years by <1 SE. To test

the male survival hypothesis, we calculated the mean proportion of time spent vigilant for each male. Because means were normally distributed (Shapiro-Wilk, $P > 0.05$), independent-sample t -tests (two-tailed with $P < 0.05$) were performed using STATISTICA (StatSoft, Tulsa, Oklahoma) to test for differences in vigilance between unpaired and paired males (Table 2).

The "paternity assurance" hypothesis predicted a higher frequency of paired male vigilance during the female's fertile period and when conspecifics were present. Because we had multiple observations for each individual, we performed repeated-measures analyses of variance (ANOVAs) of male vigilance. Models were fitted with maximum-likelihood estimation using program R, following Venables and Ripley (2002). The proportion of time that males were vigilant during feeding and resting bouts were analyzed separately. We included Julian date as a covariate to control for the possibility of seasonal effects on male vigilance, such as an increase in predation risk with seasonal time. However, because "fertile state" also controls for seasonal time, we included models without Julian date for comparison. We first fitted complete models with the main factors (habitat type, conspecific presence, fertile state, and Julian date) and relevant interaction terms that could be estimated with the available data (conspecifics * fertile state and conspecifics * habitat interactions) as fixed (between-subject) effects and habitat, conspecific presence, and fertile state as random (within-subject) effects. Residuals from this model were approximately normally distributed. We then selected the best

TABLE 2. Time-activity budgets of Harlequin Ducks during the preincubation period in Labrador, May and June, 2000–2001. Numbers in bold indicate statistical difference across sex and paired status. Standard errors are in parentheses.

	<i>n</i>	Time (%) ^a				
		Feed	Rest	Preen	Vigilance	Other ^b
Paired females	12	0.35 (0.01)	0.34 (0.02)	0.15 (0.01)	0.04 (0.01)	0.12 (0.01)
Paired males	16	0.31 (0.02)	0.29 (0.02)	0.10 (0.01)	0.19 ^c (0.02)	0.11 (0.01)
Unpaired males	6	0.37 (0.04)	0.34 (0.05)	0.10 (0.01)	0.05 (0.01)	0.14 (0.02)

^a Four hundred and fifty-four observations (217 h) of 12 paired females and 16 paired males. Sixty-one observations (29 h) of six unpaired males.

^b Locomotion, courtship-copulation, aggression, and alert (flocking behavior in response to disturbances).

^c Paired males spent $14 \pm 3\%$ more time vigilant than unpaired males.

model among plausible subset models using Akaike's Information Criterion (AIC).

To analyze patterns of male vigilance during feeding, we started by comparing the AIC values of the most complete model with and without Julian date as a covariate (feed-complete and feed-complete-no-Julian, respectively; Table 3). Because the AIC values were very similar, we removed Julian date and fixed-effects terms with nonsignificant *P* values, which resulted in model feed-subset-1. Because the random effects for conspecifics and fertile state were small proportions of the total variance for both models, these were eliminated, resulting in model feed-subset-2 (Table 3). For comparison, we included a null model (only random effects, only fixed effects). In the analysis of male vigilance during resting, none of the terms in the complete model (rest-complete; Table 3) was significant, and the AIC values were very similar between the complete model with and without Julian date as a covariate (rest-complete-no-Julian; Table 3). Because one or two factors may have been significant alone, we analyzed a variety of plausible subset models. Those models that scored reasonably well are presented in Table 3. The best models to explain variation in male vigilance during feeding and resting bouts are presented in Table 4.

RESULTS

If vigilance served to improve their own survival, we predicted that paired and unpaired males would spend the same amount of time vigilant. Averaged across all observations, paired male Harlequin Ducks were vigilant $\sim 4\times$ more frequently than either paired females or unpaired males (Table 2). Otherwise, there were relatively small differences in other behaviors between the groups.

For male vigilance during feeding, AIC showed the most support for model subset 2 (Table 3). The relatively high standard deviation of the random-effects intercept and habitat terms indicates that individual males varied substantially in average vigilance (proportion of time vigilant) in the lake habitat (-0.17 to $+0.23$ different from the mean of 0.24) but showed little variation in the stream habitat. Of nine males observed in both habitats, all were more vigilant in the lake habitat while feeding, but three males were only slightly more vigilant (range: $+0.01$ to $+0.08$), whereas the remaining

TABLE 3. Results of model comparisons using AIC for repeated-measures ANOVA of male vigilance during feeding and resting bouts.

Model	df	AIC
Feed-		
complete ^a	18	-506.4
complete-no-Julian ^a	17	-507.3
subset-1 ^a	15	-509.3
subset-2 ^a	8	-520.6
null	3	-355.3
Rest-		
complete ^b	18	-263.1
complete-no-Julian ^b	17	-263.8
subset-1 ^b	11	-274.5
subset-2 ^b	6	-278.2
subset-3 ^b	4	-279.3
null ^b	3	-270.0

^aFeed-complete = random effects of habitat, conspecifics, and fertile state. Feed-complete-no-Julian = fixed effects of habitat, conspecifics, fertile state, Julian date, conspecifics * fertile state and conspecifics * habitat interactions. Feed-subset-1 = random effects of habitat, conspecifics, and fertile state; fixed effects of habitat, conspecifics, and conspecifics * habitat interaction. Feed-subset-2 = random effects of habitat; fixed effects of habitat, conspecifics, and conspecifics * habitat interaction. Feed-null = random effects intercept, fixed effects intercept.

^bRest-complete = random effects of habitat, conspecifics, and fertile state. Rest-complete-no-Julian = fixed effects of habitat, conspecifics, fertile state, Julian date, conspecifics * fertile state and conspecifics * habitat interactions. Rest-subset-1 = random effects of habitat, and fertile state; fixed effects of conspecifics, fertile state, and conspecifics * fertile state. Rest-subset-2 = random effects of conspecifics; fixed effects of conspecifics. Rest-subset-3 = fixed effects of conspecifics. Rest-null = random effects intercept, fixed effects intercept.

six males spent, on average, at least 16% more time vigilant (range: $+0.16$ to $+0.35$). The effect of conspecifics was nearly the same on all males. In the absence of conspecifics, male vigilance during feeding was 0.19 ± 0.04 greater in the lake versus the stream habitat. Conspecifics reduced male vigilance by 0.11 ± 0.04 in the lake habitat, but there was almost no effect of conspecifics in the stream habitat on male vigilance during feeding (Fig. 1 and Table 4).

For male vigilance during resting, none of the models was significantly different from the complete model. Thus, the coefficient of the null model was used to estimate the amount of time males were vigilant during resting (0.14 ± 0.01). Model subset 3 received the most support from AIC (Table 3). This best model did not include habitat, Julian date, or fertile state as important effects on male vigilance during resting. The

TABLE 4. Repeated-measures ANOVA results for models (1) feed-subset-2 and (2) rest-subset-3. See Table 3 for descriptions of model parameters.

Model	Random effects	SD	Fixed effects	Coefficient	SE
Feed-subset-2	Intercept	0.13	Intercept	0.24	0.04
	Habitat	0.12	Habitat	-0.19	0.04
	Residual	0.10	Conspecifics	-0.11	0.03
			Habitat * conspecifics	0.11	0.04
Rest-subset-3	Intercept	0.03	Intercept	0.11	0.01
	Residual	0.15	Conspecifics	0.06	0.02

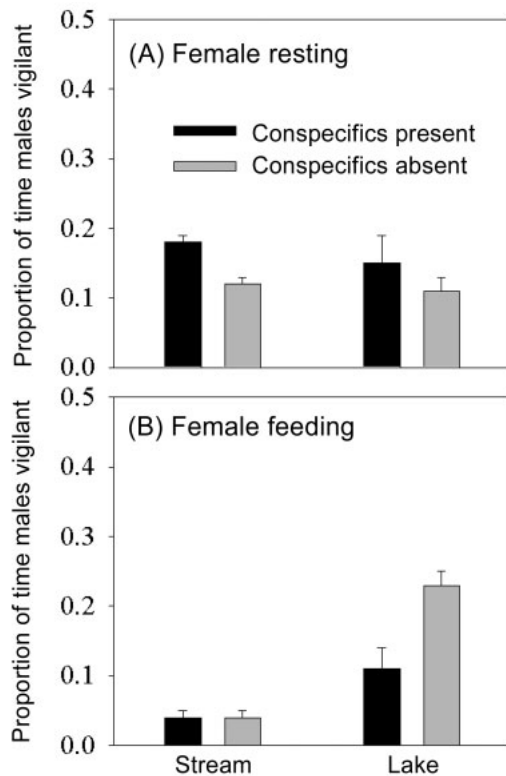


FIG. 1. Proportion of time (mean \pm SE) paired male Harlequin Ducks were vigilant (A) while females rested and (B) while females fed in stream and lake habitat while conspecifics were present or absent. There was no significant effect of habitat on male vigilance during resting. The presence of conspecifics increased the frequency of male vigilance during resting by 0.06 ± 0.02 . In the absence of conspecifics, male vigilance during feeding was 0.19 ± 0.04 greater in the lake versus the stream habitat. Conspecifics reduced male vigilance by 0.11 ± 0.04 in the lake habitat, but there was no effect of conspecifics in the stream habitat on male vigilance during feeding.

Presence of conspecifics increased vigilance during resting by 0.06 ± 0.02 , but this difference was not statistically significant (Fig. 1 and Table 4).

We predicted a positive correlation between the frequency of male vigilance and female feeding and resting, given the hypothesis that male vigilance enhances female nutritional status. Figure 2 shows a significant positive correlation between the mean proportion of time that males were vigilant and the mean proportion of time that females fed, but only in lake habitat. There was no correlation between male vigilance and female resting in either habitat (Spearman's rank correlation: lake: $r_s = 0.11$, $P = 0.77$, $n = 8$ pairs; stream: $r_s = 0.13$, $P = 0.69$, $n = 12$ pairs). There was no correlation between the mean proportion of time that paired males were vigilant and clutch initiation dates ($r_s = 0.14$, $P = 0.62$, $n = 13$ pairs).

DISCUSSION

More frequent vigilance by paired males than by females in socially monogamous species has typically been assumed to benefit males, either to ensure their survival or as a mate-guarding tactic to assure paternity. The hypothesis that males in breeding plumage are more susceptible to predation has been supported by several studies (e.g., Huhta et al. 2003), but another study found support for an alternative hypothesis that conspicuous males deter predators (Götmark 1992). In the present study, paired male Harlequin Ducks were $\sim 4\times$ more vigilant than their social partners and unpaired males during the preincubation period. The relatively infrequent vigilance by unpaired male Harlequin Ducks in breeding plumage does not support the hypothesis that paired males were vigilant to ensure their own survival. A test of the "male survival" hypothesis

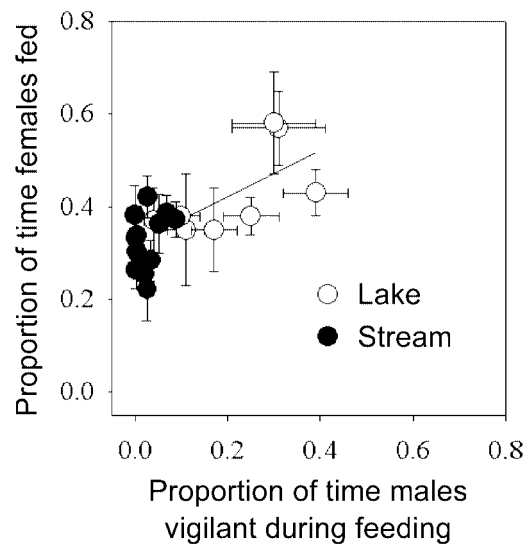


FIG. 2. Proportion of time (mean \pm SE) that female Harlequin Ducks spent feeding in relation to mean proportion of time their mates spent vigilant in stream and lake habitats during the pre-incubation period (Spearman's rank correlation: stream, $r_s = 0.26$, $P = 0.42$, $n = 12$ pairs; lake, $r_s = 0.71$, $P = 0.05$, $n = 8$ pairs). Lake means were calculated using observations collected when conspecifics were not within sight of the focal pair.

was also rejected in Eurasian Wigeons (*Anas penelope*), because in that species paired males in breeding plumage were 5 \times more vigilant than unpaired males in breeding plumage (Guillemain et al. 2003). In both studies, it is also possible that paired males were of higher quality and better able to meet the energetic requirements of frequent vigilance to ensure their own survival than unpaired males.

Mate-guarding or male accompaniment of the female before incubation is assumed to be the most common strategy by which male birds avoid cuckoldry and ensure their paternity. This hypothesis is based on observations that in the fertile period, males follow more often and remain closer to their mates than at other breeding stages (Birkhead and Møller 1992, Birkhead 1998). Several other male behaviors are believed to function as strategies to ensure paternity, including vigilance, aggression, frequent copulation, and territorial singing (Birkhead and Møller 1992). Vigilance is believed to function either as a surveillance mechanism or as a

deterrent cue to minimize the EPC attempts of other males (e.g., Brodsky 1988).

Tests for alternative functions of mate-guarding behaviors have been infrequent (Martin 1984, Artiss and Martin 1995, Stamps 1997). The assumption that the function of mate-guarding behaviors is to ensure paternity remains prevalent, despite arguments made >20 years ago for tests of alternative functions, because females also follow their mates and fertile females are not accompanied 100% of the time in many bird species (Fitch and Shugart 1984). Further, some males continue to follow their mates after the fertile period (Martin 1984). The prevalence of this assumption is perhaps even more puzzling, given relatively recent findings that higher levels of mate-guarding do not result in reduced extrapair paternity, which suggests that mate-guarding is not an effective strategy to ensure paternity or that it does not function solely or at all in ensuring paternity (Martin 1984, Kempenaers et al. 1995, Stutchbury and Neudorf 1997, Johnsen et al. 1998, Møller and Ninni 1998).

Some researchers address "female benefits" hypotheses by predicting that females should follow males as frequently as the reverse (Birkhead and Møller 1992). On finding following was male-biased, those authors rejected female benefits hypotheses as explanations for male attendance. However, if male attendance functions to enhance female nutritional status and survival and is a sexually selected trait, then males are under selective pressure to follow their social mates. Therefore, female benefits hypotheses also predict male-biased following, and associated behaviors like vigilance and aggression. If female nutritional requirements for clutch formation are highest during egg laying, which comprises most of the fertile period, then observations of higher levels of male mate-guarding when females are fertile also support the "female nutritional status" hypothesis. Thus, female benefits hypotheses have been inadequately addressed in past studies of mate-guarding.

We found little support for the paternity assurance hypothesis, because paired males were most vigilant when other males were not within sight and males were not more vigilant during the female's fertile period. During resting bouts, males were more vigilant ($0.06 \pm 0.01\%$) in the presence of conspecifics, though this difference was not statistically significant. This small additional investment by males in

vigilance may indicate that males are vigilant to ensure paternity during resting bouts; but at other times, males likely used other behaviors to ensure paternity. Both pair members position themselves between mates and sexual rivals, a behavior likely used for mate-guarding (Lazarus et al. 2004). Males may use aggression to ensure paternity, but aggression is likely an infrequent strategy toward that end, because it is rarely observed in Harlequin Ducks (Inglis et al. 2000, Squires 2003). Most aggression observed here was low-level, simultaneous "head nodding" by both pair members and was likely used to defend feeding and resting areas. Most attacks (12 of 14) observed were by paired males on paired males during feeding bouts, which suggests that attacking males were mate-guarding. However, no attacks occurred during resting bouts, despite the proximity (<1 m) of resting birds, which alternatively suggests that attacking males were defending feeding areas. Males may ensure paternity by maintaining proximity to females, as observed in synchronous diving bouts in which the male almost always follows the female (e.g., Torres et al. 2002). Aggression and following behavior require further testing to determine relationships with paternity assurance.

Males may also be vigilant as an indirect investment in paternity via maintenance of the pair bond. If females benefit from male vigilance and assess males on the quality of their vigilance, females paired to vigilant males may be less willing to engage in EPC or pair with other males. Mate-switching by females during the preincubation period has occurred in this species (Squires 2003). Thus, male vigilance may also function to ensure paternity through maintenance of the pair bond.

Insufficient food and nutrient reserves before incubation can limit egg production by females reliant on exogenous resources for egg production (income breeders; Ankney and Afton 1988, Meijer et al. 1989). Energy amassed during the preincubation period is also critical for successful incubation in many waterfowl species (Ankney et al. 1991). Unlike in altricial species, the hypothesis that male mate-guarding benefits females has been prevalent in the literature on precocial species and has been used to explain pairing before breeding in migratory ducks (Rohwer and Anderson 1988). Male aggression may enhance the foraging efficiency of female

waterfowl through defense of foraging areas and through protection of the female in species with high levels of female harassment, whereas male vigilance may enhance female survival and allow females to spend more time feeding (McKinney 1986, Black et al. 1996). In the present study, females paired to vigilant males did not initiate clutches earlier, which suggests that female reproductive performance was not strongly influenced by male vigilance. However, a recent study found that female Harlequin Ducks acquire almost all the nutrients for clutch formation from streams during the preincubation period (Bond 2005). In our study area, clutch formation was evident for all paired females that were captured, but brood production was highly variable, ranging from 10% to 89% (Goudie and Jones 2005). Male investment in the ability of females to forage and rest efficiently during the preincubation period may be critical for successful clutch formation and subsequent nest attendance. Thus, a relationship between male vigilance and clutch initiation may be revealed in future studies with higher sample sizes that control for the effects of female age and body condition on timing of clutch initiation, as well as annual variation in environmental conditions.

Our observations supported the female survival hypothesis to explain the function of male vigilance. Paired males were more vigilant than unpaired males and females, were not more vigilant when females were most fertile, and were highly vigilant when pairs were alone. Paired males may have adjusted vigilance levels according to perceived predation risk. We observed that males invested the same small amount of time (<5%) to vigilance as their mates and unpaired males during feeding bouts in the stream habitat, which suggests that feeding in fast-moving water in the middle of watercourses is less risky. This small investment in vigilance by all Harlequin Ducks may have been a baseline level of vigilance under low predation risk. Thus, in the presence of conspecifics, paired males did not decrease investment in vigilance further. By contrast, paired males were vigilant, on average, ~4× more frequently when their social partners fed in slow-moving water at lake edges rather than in the fast-moving stream habitat. Further, at lake edges, males spent less time vigilant when other birds were nearby, which suggests that feeding at lakeshores was risky but less risky in the presence of conspecifics when males

could benefit from group vigilance. Most, but not all, males invested significantly more time in vigilance while pairs fed along lakeshores. Males that did not invest more time in vigilance may have been of lower quality. During resting bouts, males maintained a relatively constant level of vigilance (14% of the time), irrespective of habitat type. Harlequin Ducks rested about the same distance from shore in both the stream and lake habitats, which suggests that resting in slow-moving water is not more risky than resting in fast-moving water. We also found support for the female nutritional status hypothesis, because females paired to vigilant males fed more often than those paired to less vigilant males when in slow-moving water close to the water's edge. There was no correlation between male vigilance and female feeding in fast-moving, midstream water because males spent only a small amount of time vigilant in streams. Because males maintained relatively constant levels of vigilance, irrespective of the amount of time females rested, there was also no correlation between male vigilance and female resting. Thus, we conclude that paired male Harlequin Ducks are vigilant to ensure the survival and nutritional status of their social partners, particularly when risk of predation is high.

ACKNOWLEDGMENTS

We are grateful to F. Cooke, R. Elner, P. Marshall, and the late Jamie Smith for valuable input into earlier versions of the manuscript, and to D. Huggard, D. Lank, and two anonymous reviewers for revisions to this version. We thank M. Kellner, S. MacLachlan, Z. Gale, C. Jones, A. Robinson, and N. Temmel for excellence in field assistance; T. Jung for logistical support; and A. Storey for her support. Personal support was provided to K.A.S. by the Natural Sciences and Engineering Research Council of Canada (NSERC). Funding was provided by the Institute for Environmental Monitoring and Research, Northern Studies Training Program, Canadian Wildlife Service, Atlantic Cooperative Wildlife Ecology Research Network, and an NSERC grant to K.M.

LITERATURE CITED

- ALISAUSKAS, R. T., AND C. D. ANKNEY. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30–61 in *Ecology and Management of Breeding Waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- ANKNEY, C. D., AND A. D. AFTON. 1988. Bioenergetics of breeding Northern Shovelers: Diet, nutrient reserves, clutch size, and incubation. *Condor* 90:459–472.
- ANKNEY, C. D., A. D. AFTON, AND R. T. ALISAUSKAS. 1991. The role of nutrient reserves in limiting waterfowl reproduction. *Condor* 93:1029–1032.
- ARTISS, T., W. M. HOCHACHKA, AND K. MARTIN. 1999. Female foraging and male vigilance in White-tailed Ptarmigan (*Lagopus leucurus*): Opportunism or behavioural coordination? *Behavioral Ecology and Sociobiology* 46: 429–434.
- ARTISS, T., AND K. MARTIN. 1995. Male vigilance in White-tailed Ptarmigan, *Lagopus leucurus*: Mate guarding or predator detection? *Animal Behaviour* 49:1249–1258.
- ASHCROFT, R. E. 1976. A function of the pair bond in the Common Eider. *Wildfowl* 27: 101–105.
- BENGSTON, S.-A. 1972. Breeding ecology of the Harlequin Duck, *Histrionicus histrionicus* (L.) in Iceland. *Ornis Scandinavica* 3:1–19.
- BIRKHEAD, T. R. 1998. Sperm competition in birds: Mechanisms and function. Pages 579–622 in *Sperm Competition and Sexual Selection* (T. R. Birkhead and A. P. Møller, Eds.). Academic Press, London.
- BIRKHEAD, T. R., AND A. P. MØLLER. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. Academic Press, London.
- BLACK, J. M. 2001. Fitness consequences of long-term pair bonds in Barnacle Geese: Monogamy in the extreme. *Behavioral Ecology* 12:640–645.
- BLACK, J. M., S. CHOUDHURY, AND M. OWEN. 1996. Do Barnacle Geese benefit from lifelong monogamy? Pages 91–117 in *Partnerships in Birds: The Study of Monogamy* (J. M. Black, Ed.). Oxford University Press, New York.
- BOND, J. C. 2005. Nutrient acquisition and allocation strategies for reproduction by female Harlequin Ducks. M.Sc. thesis, Simon Fraser University, Burnaby.
- BRODSKY, L. M. 1988. Mating tactics of male Rock Ptarmigan, *Lagopus mutus*: A conditional

- mating strategy. *Animal Behaviour* 36: 335–342.
- CAREY, C. 1996. Female reproductive energetics. Pages 324–374 in *Avian Energetics and Nutritional Ecology* (C. Carey, Ed.). Chapman and Hall, New York.
- CHOUDHURY, S., AND J. M. BLACK. 1993. Mate-selection behaviour and sampling strategies in geese. *Animal Behaviour* 46:747–757.
- CHRISTENSEN, T. K. 2000. Female pre-nesting foraging and male vigilance in Common Eider *Somateria mollissima*. *Bird Study* 47:311–319.
- DAHLGREN, J. 1990. Females choose vigilant males: An experiment with the monogamous Grey Partridge, *Perdix perdix*. *Animal Behaviour* 39:646–651.
- FITCH, M. A., AND G. W. SHUGART. 1984. Requirements for a mixed reproductive strategy in avian species. *American Naturalist* 124: 116–126.
- GAUTHIER, G. 1987. The adaptive significance of territorial behaviour in breeding Buffleheads: A test of three hypotheses. *Animal Behaviour* 35:348–360.
- GAUTHIER, G., AND J. TARDIF. 1991. Female feeding and male vigilance during nesting in Greater Snow Geese. *Condor* 93:701–711.
- GÖTMARK, F. 1992. Anti-predator effect of conspicuous plumage in a male bird. *Animal Behaviour* 44:51–55.
- GOUDIE, R. I., AND I. L. JONES. 2005. Feeding behavior of Harlequin Ducks (*Histrionicus histrionicus*) breeding in Newfoundland and Labrador: A test of the food limitation hypothesis. *Bird Behavior* 17:9–18.
- GUILLEMAIN, M., R. W. G. CALDOW, K. H. HODDER, AND J. D. GOSS-CUSTARD. 2003. Increased vigilance of paired males in sexually dimorphic species: Distinguishing between alternative explanations in wintering Eurasian Wigeon. *Behavioral Ecology* 14:724–729.
- HANNON, S. J., AND K. MARTIN. 1992. Monogamy in Willow Ptarmigan: Is male vigilance important for reproductive success and survival of females? *Animal Behaviour* 43:747–757.
- HUHTA, E., S. RYTKÖNEN, AND T. SOLONEN. 2003. Plumage brightness of prey increases predation risk: An among-species comparison. *Ecology* 84:1793–1799.
- HUNT, W. A. 1998. The ecology of Harlequin Ducks *Histrionicus histrionicus* breeding in Jasper National Park, Canada. M.Sc. thesis, Simon Fraser University, Burnaby.
- INGLIS, I. R., J. LAZARUS, AND R. TORRANCE. 1989. The pre-nesting behaviour and time budget of the Harlequin Duck *Histrionicus histrionicus*. *Wildfowl* 40:55–73.
- INGLIS, I. R., J. LAZARUS, AND R. TORRANCE. 2000. Breeding status and aggressive communication in the Harlequin Duck *Histrionicus histrionicus*. *Wildfowl* 51:139–153.
- JOHNSON, A., J. T. LIFJELD, P. A. ROHDE, C. R. PRIMMER, AND H. ELLEGREN. 1998. Sexual conflict over fertilizations: Female Bluethroats escape male paternity guards. *Behavioral Ecology and Sociobiology* 43:401–408.
- JÖNSSON, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78:57–66.
- KEMPENAERS, B., G. R. VERHEYEN, AND A. A. DHONDT. 1995. Mate guarding and copulation behaviour in monogamous and polygynous Blue Tits: Do males follow a best-of-a-bad-job strategy? *Behavioral Ecology and Sociobiology* 36:33–42.
- LAMPRECHT, J. 1989. Mate guarding in geese: Awaiting female receptivity, protection of paternity, or support of female feeding? Pages 48–60 in *The Sociobiology of Sexual and Reproductive Strategies* (A. E. Rasa, C. Vogel, and E. Voland, Eds.). Chapman and Hall, London.
- LAZARUS, J., I. R. INGLIS, AND R. L. F. TORRANCE. 2004. Mate guarding conflict, extra-pair courtship and signalling in the Harlequin Duck, *Histrionicus histrionicus*. *Behaviour* 141:1061–1078.
- MARTIN, K. 1984. Reproductive defence priorities of male Willow Ptarmigan (*Lagopus lagopus*): Enhancing mate survival or extending paternity options? *Behavioral Ecology and Sociobiology* 16:57–63.
- MARTIN, P., AND P. BATESON. 1986. *Measuring Behaviour: An Introductory Guide*. Cambridge University Press, Cambridge, United Kingdom.
- McKINNEY, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks. Pages 153–171 in *Ecological Aspects of Social Evolution: Birds and Mammals* (D. I. Rubenstein and R. W. Wrangham, Eds.). Princeton University Press, Princeton, New Jersey.
- MEIJER, T., D. MASMAN, AND S. DAAN. 1989. Energetics of reproduction in female kestrels. *Auk* 106:549–559.

- MØLLER, A. P., AND P. NINNI. 1998. Sperm competition and sexual selection: A meta-analysis of paternity studies of birds. *Behavioral Ecology and Sociobiology* 43:345–358.
- PIETZ, P. J., D. A. BRANDT, G. L. KRAPU, AND D. A. BUHL. 1995. Modified transmitter attachment method for adult ducks. *Journal of Field Ornithology* 66:408–417.
- PIZZARI, T. 2003. Food, vigilance, and sperm: The role of male direct benefits in the evolution of female preference in a polygamous bird. *Behavioral Ecology* 14:593–601.
- ROBERTSON, G. J., AND R. I. GOUDIE. 1999. Harlequin Duck (*Histrionicus histrionicus*). In *The Birds of North America*, no. 466 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- RODWAY, M. S. 1998. Activity patterns, diet, and feeding efficiency of Harlequin Ducks breeding in northern Labrador. *Canadian Journal of Zoology* 76:902–909.
- ROHWER, F. C., AND M. G. ANDERSON. 1988. Female biased philopatry, monogamy, and the timing of pairing in migratory waterfowl. Pages 187–221 in *Current Ornithology*, vol. 5 (R. F. Johnston, Ed.). Plenum Press, New York.
- SQUIRES, K. A. 2003. Pre-incubation behavior of Harlequin Ducks (*Histrionicus histrionicus*) in Labrador: Testing the function of male vigilance and aggression. M.Sc. thesis, University of British Columbia, Vancouver.
- STAMPS, J. 1997. The role of females in extrapair copulations in socially monogamous territorial animals. Pages 294–319 in *Feminism and Evolutionary Biology: Boundaries, Intersections, and Frontiers* (P. A. Gowaty, Ed.). Chapman and Hall, New York.
- STUTCHBURY, B. J. M., AND D. L. NEUDORF. 1997. Female control, breeding synchrony, and the evolution of extra-pair mating systems. Pages 103–121 in *Avian Reproductive Tactics: Female and Male Perspectives* (P. G. Parker and N. T. Burley, Eds.). Ornithological Monographs, no. 49.
- TEUNISSEN, W., B. SPAANS, AND R. DRENT. 1985. Breeding success in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. *Ardea* 73:109–119.
- TORRES, R., F. COOKE, G. J. ROBERTSON, AND W. S. BOYD. 2002. Pairing decisions in the Harlequin Duck: Costs and benefits. *Waterbirds* 25:340–347.
- VENABLES, W. N., AND B. D. RIPLEY. 2002. *Modern Applied Statistics with S*, 4th ed. Springer-Verlag, New York.

Associate Editor: K. Yasukawa