

Pair-Bond Defense Relates to Mate Quality in Harlequin Ducks (*Histrionicus histrionicus*)

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Pair-bond Defense Relates to Mate Quality in Harlequin Ducks (*Histrionicus histrionicus*)

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Abstract.—Previous theory to explain pairing behavior in waterfowl suggested that timing of pairing was constrained by costs to males of being paired and assumed that males incur most of the cost of defense after a pair bond is formed. An alternative hypothesis predicts that male and female partners will mutually defend their pair bond and that an individual will assume a greater share of defense when paired to a relatively high than low quality partner. Behavior of wintering Harlequin Duck (*Histrionicus histrionicus*) pairs was consistent with the latter hypothesis. Females and males shared equally in pair-bond defense in new pairs involving young females, while males assumed a greater share of defense when paired to an older female. Overall, males performed more aggressive displays in defense of the pair bond than females, but displays by females were more frequently of higher intensity than those of their mate. The relative share of pair-bond defense also varied between females and males depending on the target of the aggressive display. In some pairs, females performed virtually all defensive displays and bore the primary cost of pair-bond defense. Even when sex ratios are male-biased, differences in male quality probably make females willing to protect a pair bond with a high-quality male. Mutual mate choice and shared defense of a pair bond indicated that “pair-bond defense” would be a more appropriate label than “mate-defense” for the mating system of Harlequin Ducks and likely most monogamous avian species. Received 18 November 2012, accepted 1 February 2013.

Key words.—agonistic display, divorce, Harlequin Duck, *Histrionicus histrionicus*, male mate choice, mate-defense, mating system, monogamy, mutual-choice hypothesis, pair-bond defense.

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Mating systems have been classified in relation to the potential of individuals, most commonly males, to monopolize mates or resources required by mates (Emlen and Oring 1977; Oring 1982), and the ability of mates, generally females, to resist such control (Gowaty 1996). This has led to the oversimplified dichotomy of resource-defense and mate-defense categories (McKinney 1986; Ostfeld 1987). In migratory waterfowl, female mate choice is unrelated to resource defense by males and mate-guarding by males is common (McKinney 1986). Their mating system has thus been variously described as “mate-defense” (Oring 1982; Anderson et al. 1992; Robertson et al. 2000), “female-defense monogamy” (Wittenberger 1979; Wittenberger and Tilson 1980), or as “monogamy through coercion” (Johnson and Burley 1997), misleading labels because they imply male control (McKinney 1986). The “male-costs hypothesis” to explain pairing behavior in waterfowl was a logical extension of this classification and suggested that pairing benefits both sexes but is constrained by costs to males of courtship, mate

defense, and vigilance (Rohwer and Anderson 1988; Owen and Black 1990; Oring and Saylor 1992). The hypothesis assumed that males incur most of the cost of defense once a pair bond is formed, even though some studies had shown that females may perform as much or more pair-bond maintenance and defense as males (Weller 1967; Anderson 1984; Lovvorn 1989).

Relative parental investment and intrasexual competition among males for females likely place females in control of pairing in most waterfowl species (Trivers 1972; McKinney 1986; Black and Owen 1988; Oring and Saylor 1992). However, ample evidence of choosiness by females (Wishart 1983; Bossema and Roemers 1985; Sorenson and Derickson 1994; Omland 1996) implies variance in male mate quality (Lovvorn 1990) and, because there is known variance in female mate quality in relation to age and other phenotypic traits (Rohwer 1992), theory predicts male as well as female choosiness and mate preference functions that are relative to an individual’s own quality and expectations of pairing (Parker 1983). Rela-

tive defense of the pair bond by male and female partners, extra-pair courtship, divorce, and search for extra-pair copulations may be related to the match between preferred and realized mate choice for each partner (Petrie and Hunter 1993; Choudhury 1995; Ens et al. 1996; Spooner et al. 2004). Variation in that match likely predicts variation in behavior among pairs, such as higher mate attendance by some males (e.g., Ashcroft 1976; Scott 1980).

Once formed, a pair bond is perhaps best considered as a resource held with varying value by each partner and entailing conflicts of interest between the two participants in relation to its maintenance and defense. The "mutual-choice hypothesis" (Rodway 2007a, 2007b) predicts that male and female partners will engage in mutual defense of their pair bond, and that an individual will assume a greater share of defense when paired to a relatively high than low quality partner. This prediction had not previously been tested and was a main focus of this study. Because the function of agonistic displays likely varies depending on context (Bradbury and Vehrencamp 1998), the proportion of pair-bond defense performed by female and male partners also may vary in relation to the target of aggressive displays. I investigated differences between partners in the frequency and types of display directed at individuals of different age and sex classes. Behavior following breaking of the pair bond was also investigated to test the predictions that either sex may initiate divorce and that divorce is related to mate quality (Ens et al. 1996). I used age as a measure of mate quality (Rohwer 1992).

An important assumption of the mutual-choice hypothesis is that males are unable to coercively sequester females. Lack (1968) suggested that males control pairing in waterfowl and assumed that male ducks can sequester females through mate-guarding behavior and may obtain a mate through scramble competition or male-male competition with success related to dominance status (Wynne-Edwards 1962). Male dominance rank has been correlated with pairing success, suggesting that male-male competition may sometimes constrain female

choice (Brodsky et al. 1988), but more often male dominance has been unrelated to female choice (Bossema and Roemers 1985) and high dominance rank has been a consequence of pairing success rather than a cause (Raveling 1970; Patterson 1977; Lamprecht 1986; but see Hepp 1989). I thus predicted that unpaired females can effectively signal mate-choice preferences and deter courting males.

Harlequin Ducks (*Histrionicus histrionicus*) have a monogamous mating system with no paternal care and form multi-year pair bonds on their wintering grounds (Gowans et al. 1997; Smith et al. 2000). Both sexes begin courtship during their first winter, most female Harlequin Ducks pair in their second year, and males rarely pair before their fourth winter (Rodway 2007b). Harlequin Ducks have a male-biased sex ratio of 1.5:1 in the Pacific Northwest (Rodway et al. 2003a), and males have a variable Alternate I plumage that makes them identifiable throughout their first winter (Smith et al. 1998). Harlequin Ducks generally winter in small groups of 2-20 along rocky, marine shores (Robertson and Goudie 1999) where behavioral interactions are easy to observe and individuals can be captured and marked. They are thus an ideal study species to test predictions of the mutual-choice hypothesis in relation to pair-bond defense, divorce, and female control during courtship.

METHODS

Marking and Aging

About 3,500 Harlequin Ducks were caught in drive traps during molt in August and September from 1992-2000. They were individually marked with alpha-numeric colored leg bands at five locations in the Strait of Georgia, British Columbia, as part of a joint effort between the Canadian Wildlife Service and Simon Fraser University (details in Robertson et al. 1998; Rodway et al. 2003b). Unique, shape-color-combination nasal discs were also put on 457 birds, most in 1998-1999, and a few in 1997 and 2000, at three banding sites in the northern Strait of Georgia, British Columbia. Nasal discs decreased pairing success of males and increased mate change in previously paired females but did not affect other behaviors (Regehr and Rodway 2003). Captured

tright 1942). Four age classes were discriminated: first, second, and third year, and after third year (Smith et al. 1998; Mather and Esler 1999). Birds were considered first- (1Y), second- (2Y), and third-year (3Y) throughout their first, second, and third winters, respectively, and after-third-year (A3Y) afterwards. In some cases, I only distinguish between first-year (1Y) and after-first-year (A1Y) birds.

Behavioral Observations

Continuous observations of focal individuals (Altmann 1974) were conducted throughout daylight hours during the winters of 1998-2000 to determine the type and frequency of social interactions (details in Rodway 2006, 2007b). Pair status was judged based on observed

The trounce was mostly used by females, especially to deter A1Y males, and I never observed it used by unpaired 1Y or A1Y males (Table 1). As with 1Y females, aggressive displays sometimes deterred approaching or courting males and sometimes acted to incite courting males. Even the most aggressive trounce varied in its effect, sometimes deterring a party of courting males and ending courtship, and sometimes deterring only the specific male attacked. It appeared that females were at times unwilling to engage in courtship and could effectively signal that unwillingness to approaching males, while at other times the displays by females were intended to communicate mate-choice preferences.

Both sexes participated in pair-bond de-

Table 2. Frequency of aggressive displays by female and male partners of Harlequin Duck pairs in relation to the recipient of the aggressive signal. Paired observations (n = 764) were compared using 2-tailed, paired t-tests. Chases between mates were included but low-intensity, intra-pair displays were excluded (see Methods).

| Recipient | Number of Aggressive Displays per Hour by | | | t | P |
|---------------|---|--------------|--|------|-------|
| | Female of Pair | Male of Pair | | | |
| Female | 0.17 ± 0.05 | 0.29 ± 0.06 | | -1.8 | 0.075 |
| 1Y male | 0.19 ± 0.05 | 0.07 ± 0.02 | | 2.4 | 0.017 |
| A1Y male | 2.21 ± 0.30 | 4.87 ± 0.37 | | -6.6 | 0.000 |
| Own mate | 0.04 ± 0.02 | 1.32 ± 0.13 | | -9.8 | 0.000 |
| Other species | 0.23 ± 0.07 | 0.31 ± 0.08 | | -0.7 | 0.469 |
| Total | 2.82 ± 0.33 | 6.87 ± 0.45 | | -8.6 | 0.000 |

The types of display used by female and male partners also varied in relation to the target of the display (Table 1). The most intense displays (chases and trounces) directed at females, 1Y males, and A1Y males, comprised 37%, 46%, and 19%, respectively, of all displays by paired females, and 29%, 29%, and 6%, respectively, of all displays by paired males. For paired females, higher intensity displays formed a greater proportion of the displays directed at females ($G_3 = 26.4, P < 0.001$) and 1Y males ($G_3 = 22.9, P < 0.001$) than at A1Y males, opposite to the trend found above for unpaired females, and a similar proportion of the displays directed at females and 1Y males ($G_3 = 2.8, P = 0.4$). For paired males, higher intensity displays also formed a greater proportion of the displays directed at females than at A1Y males ($G_3 = 89.0, P < 0.001$; there were insufficient data to test for differences involving 1Y males). Head-nods were the most frequent display performed by paired males, especially to other males (Table 1).

The proportion of pair-bond defense performed by females and males varied in relation to the age of the female. For pairs involving 2Y, 3Y, and A3Y females, the number of aggressive displays directed at other

birds was higher for 2Y than 3Y and A3Y females, but did not differ among their mates (Table 3). Paired t-tests indicated that the number of aggressive displays directed at others did not differ between partners for pairs involving 2Y and 3Y females, but for pairs involving older females, males per formed more displays in defense of the pair bond than their A3Y mates (Table 3). Paired 2Y females also were recipients of aggressive displays by others more often ($4.2 \pm 1.6 h^{-1}$) than 3Y ($1.2 \pm 0.4 h^{-1}$) and A3Y ($1.5 \pm 0.3 h^{-1}$) females ($F_{2,343} = 4.8, P = 0.009$; post-hoc: $P < 0.05$), while no differences were detected in the number of aggressive displays received by their mates ($0.5 \pm 0.5 h^{-1}, 0.3 \pm 0.2 h^{-1},$ and $0.6 \pm 0.1 h^{-1}$, for the mates of those same 2Y, 3Y, and A3Y females, respectively, $F_{2,343} = 0.4, P = 0.7$). Some of the differences in the number of interactions that paired 2Y, 3Y, and A3Y females were involved in may have been related to the frequency that they were courted ($20 \pm 6, 10 \pm 4,$ and 8 ± 2 min d, respectively), although differences in courtship time were not significant ($F_{2,343} = 2.1, P = 0.1$).

Further evidence that pairs varied in the relative share of pair-bond defense assumed by each partner came from observations of

Table 3. Frequency of aggressive displays to others by female and male partners of Harlequin Duck pairs in relation to the age of the paired female.

| Age of Female | Number of Aggressive Displays per Hour by | | | Paired t-tests | | |
|----------------|---|--------------|----------------------------|----------------|------|-------|
| | Female of Pair | Male of Pair | | n | t | P |
| 2Y | 7.5 ± 3.5 | 3.7 ± 1.3 | | 26 | 1.1 | 0.301 |
| 3Y | 0.8 ± 0.4 | 2.2 ± 0.9 | | 62 | -1.7 | 0.112 |
| A3Y | 2.2 ± 0.5 | 4.5 ± 0.7 | | 258 | -3.6 | 0.000 |
| ANOVA results: | $F_{2,343} = 6.4, P = 0.002$ | | $F_{2,343} = 1.4, P = 0.3$ | | | |

the main cost of pair-bond defense. Even when sex ratios are male-biased, differences in male quality probably makes females willing to protect a pair bond with a high-quality male (Parker 1983; Lovvorn 1990; Johnstone et al. 1996). Differences in shared defense among pairs may reflect the degree to which each partner's realized mate choice matched their preference (Petrie and Hunter 1993). This could explain why younger females performed a greater share of pair defense and were recipients of aggressive interactions more frequently than older females, and why males as well as females appeared to initiate divorce to pursue a better option (Choudhury 1995; Ens et al. 1996), in one case by moving 150 km away to a different wintering site. Females and males shared equally in pair-bond defense in new pairs involving young females, while males assumed a greater share of defense when paired to an older, presumably higher-quality female. Willingness to invest in pair-bond defense also may depend on the confidence each partner has in the security of the pair bond and their past investment in the pair bond, although a divorce rate of 3.1%, similar to that of geese and one-lake grebes (18.96% (volving 0ment inar) 1(d a greate 0.028 T18.96 -dx (v>c0.1

sible explanation for this behavior by paired females may be that they perceived a greater risk to the pair bond from intruding females than males. Paired males perhaps used high-intensity displays to intruding unpaired females to signal intentions of fidelity to their mate. Why paired females were particularly aggressive toward immature males is unclear. Did they mistake them for females, or were they forcibly rejecting clearly inferior potential mates?

Patterns of defense exhibited 24 ted gi

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