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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 Derrickson 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; Spoon *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 (Bossemma 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 birds were sexed and aged by plumage, cloacal examination, and the depth of the Bursa of Fabricius (Kor-

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 behavior (Gowans *et al.* 1997). Frequency of all agonistic interactions was recorded during each observation session. I defined five types of agonistic displays in order of increasing intensity (modified from Inglis *et al.* 1989, 2000): the *head-nod* (elliptical upward and forward movement of the head), the *bill-poke* (neck extended horizontally with bill closed), the *bill-gape* (neck extended horizontally with bill open), the *chase* (neck extended plus rush across the water at the target), and the *trounce* (jumping on the target bird and usually driving it under the water). I excluded low-intensity, intra-pair displays (head-nods and slight head-jerks) that were used during copulation and during times when pairs were initiating different behaviors, such as leaving a roost or taking flight, and included only aggressive displays (chases) between mates that were used in relation to other birds (typically the male chasing his mate away from other males).

Statistical Analyses

I used G-tests to compare frequencies of different types of displays among age-, sex-, and pair-status classes. Total numbers of agonistic interactions per observation session were compared among classes using t-tests and one-way ANOVA followed by Tukey post-hoc tests, except Wilcoxon Signed Ranks Test was used when data distribution violated assumptions for parametric tests. Tolerance for Type I error was set at 5% for all tests (Sokal and Rohlf 1995).

RESULTS

I analyzed the behavior of 1Y and older, unpaired female Harlequin Ducks to determine whether males could coercively sequester females or whether females could manipulate male behavior during courtship as predicted. First-year females interacted little with males through most of the winter. During 29 observation sessions conducted October-February, I observed 1Y females mostly in all-female groups (55% of sessions), fe-

male-biased groups (28%), or alone (10%). Agonistic interactions involving 1Y females were first observed during observation sessions on 17 February and were common in March and April (7.2 ± 2.2 interactions h^{-1} , $n = 18$ observation sessions), but not as common as those that involved all other unpaired females (25.2 ± 5.2 interactions h^{-1} , $n = 79$ observation sessions; *t*-test, equal variances not assumed: $t = 3.19$, $P = 0.002$). After I first observed 1Y females being courted on 6 March, many interactions were associated with courtship (41%, $n = 71$ observation sessions). During March and April, 1Y females performed more aggressive displays to other birds (5.3 ± 2.0 h^{-1}) than they received (1.9 ± 0.6 h^{-1} ; Wilcoxon Signed Ranks Test: $Z = -2.1$, $P = 0.04$).

It was often difficult to determine the intention of various displays by 1Y females. Displays sometimes deterred males that were showing an interest: *bill-pokes* at an approaching unpaired male resulted in him turning away, and a *bill-poke* followed by a *chase* deterred a 1Y male that was following. At other times, similar displays (*bill-pokes* and *bill-gapes*) were performed to passing males that were not showing obvious interest, and I could not tell whether the female was attempting to deter or to invite male interest in those situations. During courtship, *bill-pokes* appeared to sometimes incite competition among courting males and sometimes deter males. Thus, many displays performed during March and April by 1Y females may have been associated with signaling preference or rejection of specific males rather than attempts to deter courtship *per se*.

Considering all ages, unpaired females frequently displayed aggressively at males, and they used a greater proportion of higher intensity displays to A1Y males than did all other sex-paired-status classes, including paired females (Table 1; *chases* and *trounces* combined into one category: $G_3 = 18.6$, $P < 0.001$), 1Y males ($G_3 = 47.5$, $P < 0.001$), unpaired A1Y males ($G_3 = 87.8$, $P < 0.001$), and paired males ($G_3 = 259.9$, $P < 0.001$). Unpaired females also used higher intensity displays proportionately more often to A1Y males than to females ($G_3 = 7.6$, $P = 0.05$).

Table 1. Relative frequencies of different aggressive displays performed by wintering Harlequin Ducks in relation to their sex, age [hatch-year (1Y) and after-hatch-year (AIY)], and paired status, and to the target of the display. Displays are listed in order of increasing intensity (see text). All displays between mates were excluded.

Target and Type of Display	Unpaired Female	Unpaired 1Y Male	Unpaired AIY Male	Paired Female	Paired Male
Number of displays	325	108	715	594	1477
Directed at females (%)					
Head-nod	6.5	8.3	22.1	1.2	2.6
Bill-poke	3.1	8.3	1.5	4.0	0.4
Bill gape	5.5	1.9	0.0	0.8	0.8
Chase	1.5	8.3	29.1	3.0	2.4
Trounce	0.0	0.0	0.0	0.5	0.0
Total	16.6	26.9	52.7	9.6	6.2
Directed at 1Y males (%)					
Head-nod	0.9	0.0	0.0	1.0	0.7
Bill-poke	0.9	0.9	0.0	2.0	0.0
Bill gape	1.5	7.4	0.7	1.0	0.1
Chase	2.2	0.9	0.6	3.4	0.3
Trounce	0.0	0.0	0.0	0.2	0.1
Total	5.5	9.3	1.3	7.6	1.2
Directed at AIY males (%)					
Head-nod	23.4	23.1	30.3	34.3	75.5
Bill-poke	18.8	6.5	7.6	22.4	7.1
Bill gape	18.5	34.3	2.5	10.8	4.3
Chase	16.6	0.0	5.6	14.3	5.7
Trounce	0.6	0.0	0.0	1.0	0.1
Total	77.8	63.9	46.0	82.8	92.7
Total directed all birds (%)					
Head-nod	30.8	31.5	52.4	36.5	78.8
Bill-poke	22.8	15.7	9.1	28.5	7.5
Bill gape	25.5	43.5	3.2	12.6	5.1
Chase	20.3	9.3	35.2	20.7	8.3
Trounce	0.6	0.0	0.0	1.7	0.2
Total	100.0	100.0	100.0	100.0	100.0

The *trounce* was mostly used by females, especially to deter AIY males, and I never observed it used by unpaired 1Y or AIY 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 defense as predicted. Paired comparisons between females and males in pair bonds indi-

cated that males performed more aggressive displays in defense of the pair bond than females (Table 2), but that displays by females were more frequently of higher intensity than those of their mate (Table 1; *chases* and *trounces* combined into one category: $G_3 = 336.8, P < 0.001$). The relative share of pair-bond defense varied between females and males depending on the target of the aggressive display (Table 2). Aggression directed at AIY males was more frequent by males than females, aggression to 1Y males was more frequent by females than males, and there were no differences between female and male partners in the number of aggressive displays directed at other females or at other species. Paired females were often recipients of aggressive *chases* by their mates (Table 2), which accounted for most of the aggressive interactions they received from males.

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 39%, 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 performed 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 ($4.2 \pm 1.6 \text{ h}^{-1}$) than 3Y ($1.2 \pm 0.4 \text{ h}^{-1}$) and A3Y ($1.5 \pm 0.3 \text{ h}^{-1}$) females ($F_{2,343} = 4.8, P = 0.009$; post-hoc: $P_s < 0.05$), while no differences were detected in the number of aggressive displays received by their mates ($0.5 \pm 0.5 \text{ h}^{-1}, 0.3 \pm 0.2 \text{ h}^{-1}$, and $0.6 \pm 0.1 \text{ h}^{-1}$, 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 $8 \pm 2 \text{ min d}^{-1}$, 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:	$F_{2,343} = 6.4, P = 0.002$	$F_{2,343} = 1.4, P = 0.3$			

pairs when the female was being courted. Of the few observation sessions during which paired females were courted, and I kept track of the position of their mate, the mate was always closest to the female in eight sessions and was not always closest in three sessions. Pair-bond defense was mutual in most cases. In one example, the female was courted by three to six males and performed numerous aggressive displays at these males throughout the 5-min session while her mate swam just ahead, seeming to pay little attention. Pair-bond defense performed only by the female was observed during several other observation sessions.

Mate fidelity from year to year was high. For pairs for which I knew the identity of both partners, and both were known to be still alive the next year, I had four records of divorce and 126 records of re-uniting, representing a divorce rate of 3.1% per year. Most records were of A3Y birds, but I did have three records of females and one record of a male paired as 2Y birds and re-uniting with their mates the next year. Some pairs were together for at least 5 years. Divorced pairs were together for at least 1 year (two pairs) or 2 years (two pairs) before divorcing. Females of the former two pairs were 4 years old, the latter were at least 6 years old, and all males were at least 7 years old when they divorced. Two of the divorced females and none of the divorced males were marked with nasal discs. Nasal discs had been on one younger and one older female for over a year, and, thus, if the discs were responsible for divorce, their effect was delayed 1 year. Also, the older female lost her nasal discs before divorcing, and, in contrast to the rest of the individuals that remained in their same wintering location following divorce, she moved to a different wintering site 150 km away. The former mate of this female consorted with two other females within the 3-week period after being divorced in mid-March but remained unpaired the next winter. This suggests that this female initiated divorce by moving to a different wintering location. My finding that one member of a former pair may move to a different wintering area suggests that some divorces may have been

undetected because one partner may have moved outside my study areas and thus was not known to be alive. One male that was at least 8 years old and had been paired to a non-nasal disk, 3Y female for 1 year, was, following divorce, paired for at least 2 consecutive years to a female that also was at least 8 years old. Assuming that reproductive success increases with female age (Rohwer 1992), this suggests that this male may have secured a better mate and may have been the partner that initiated the divorce.

DISCUSSION

Signaling by unpaired Harlequin Duck females was sometimes difficult to interpret but it was evident that females were capable of deterring courting males and that males could not coercively sequester females. Low intensity displays were usually sufficient to deter approaching males, but more aggressive *chases* and *trounces* were frequently used by unpaired and paired females to effectively repel individual or groups of courting males. A "*trounced*" male never continued his approach to the displaying female. The *trounce* was predominantly a female display and has not previously been described (Inglis *et al.* 1989, 2000). Paired males used it rarely to repel intruding males and I never observed it used by unpaired males. This study thus validates an important assumption of the mutual-choice hypothesis (Rodway 2007a) and demonstrates a behavioral mechanism by which female Harlequin Ducks exercise mate-choice preferences. Male mate-choice preferences were also evident. First-year females were largely ignored by males for most of the winter, and perhaps became more attractive in the spring when the probability of males pairing with older females had declined. Males exhibited preferences among older females as well (Rodway 2007b).

Relative roles of females and males in defense of their chosen pair bond varied among pairs, as predicted by the mutual-choice hypothesis (Rodway 2007a, 2007b). In some pairs females performed virtually all defensive displays and obviously bore

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 swans (Ens *et al.* 1996), indicates that most pairs persist once a mutual choice is made.

Males performed more displays in defense of the pair bond than did females, but displays by females were of higher intensity than those of their mate (as found by Inglis *et al.* 2000). Thus, it is difficult to compare the costs of mate defense for the two sexes without some measure of the cost of each type of display. Most displays performed by both partners were directed toward intruding, adult males, but partner males performed more of these than their mates did. The high proportion of displays directed at males likely indicates that adult males were much more likely than females to approach a pair. Paternity protection clearly was not an issue during winter, feeding areas were not defended (Rodway 2006), nor was female foraging efficiency improved (Rodway 2007b), and thus male and female aggression toward adult males likely functioned solely to defend the pair bond. Females were

more likely than their partners to display aggressively at immature males, while defense directed at females or other species was performed at similar rates by each partner.

Less frequent displays were directed at immature males by paired males than females is consistent with previous findings of lower-than-expected rates of aggression directed at immature males by adult males (Rodway 2006). However, it is curious that paired females exhibited high rates of aggression toward immature males. This suggests that delayed plumage maturation acts as an honest signal of subordination (Lyon and Montgomerie 1986) that minimizes aggressive interactions with adult males but not females. It is also puzzling why female and male partners used higher intensity displays more frequently to females and immature males than to adult males. Higher intensity interactions between closely-matched opponents is predicted by game theoretic models of fighting (Maynard Smith and Parker 1976), contrary to what was observed here because there is a clear asymmetry between males and females and between older, paired females and younger, unpaired females or immature males. Game theory predictions (Maynard Smith and Parker 1976) would be supported if, for females, such interactions occurred primarily between paired females. Aggression between paired females might have been expected because both paired and unpaired males frequently courted paired females (Rodway 2007b), but was rarely observed. More commonly, a paired female simply waited for her partner while he was courting another paired female, and frequently males of two or three pairs would group together to court each other's mates in turn, suggesting that inter-pair courtship was not perceived as a threat to current pair bonds and may provide some benefit to both sexes in relation to possible future pairing opportunities if a partner dies. Most high-intensity, female-oriented aggression performed by paired birds was directed at unpaired females, who typically retreated. Aggression by paired individuals toward same-sex intruders is expected in monogamous species (Cézilly *et al.* 2000), and a pos-

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 by female and male partners observed in this study indicate that describing mating systems of Harlequin Ducks and similar species with terms such as "mate-defense," "female-defense monogamy," or as "monogamy through coercion" is overly simplistic (McKinney 1986). Mating systems of waterfowl are complicated by the fact that many species pair on their wintering grounds where mate-guarding for paternity protection is irrelevant and benefits of male defense to female condition are not evident, at least for most migratory ducks (reviewed in Rodway 2007a). Mutual defense was the basic pattern observed in Harlequin Ducks with each sex more likely to address aggression toward certain types of individuals, perhaps related to their relative dominance status or to perceived risk to the pair bond. Though paired males at times guarded their mates from harassment by other males, in fact, outside of courtship activities, paired and unpaired females received similar amounts of aggression from males, and for paired females most of this aggression came from their mates (Rodway 2007b). Mutual mate choice and shared defense of a pair bond indicate that "pair-bond defense" would be a more appropriate label than "mate-defense" for the mating system of Harlequin Ducks and probably most monogamous avian species. This terminology focuses attention on the interests of both partners, recognizes variation among pairs in the relative roles of the two sexes, avoids *a priori* connotations of male control (Gowaty 1996) or male protection (Rohwer and Anderson 1988) of the female, and encourages gender-neutral interpretations (Gowaty 1997) of display function. I suggest that we

reserve the term "mate-defense" for systems where one sex can completely sequester an opposite-sex individual through mate-guarding (examples in Brown *et al.* 1997), comparable to "resource-defense" where individuals can sequester space through territorial behavior. Recent studies considering a broader diversity of avian species confirm that these are not distinct categories and that we can expect intra- and inter-specific variation in the relative roles of female and male partners in defense of territories and pair bonds (Hall 2004; Fedy and Stutchbury 2005; Stutchbury and Morton 2008), reflecting not only conflicts of interest but also obvious mutual interests between monogamous partners (Trivers 1972).

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