# BREEDING STATUS AND AGGRESSIVE COMMUNICATION IN THE HARLEQUIN DUCK *HISTRIONICUS HISTRIONICUS*

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*The breeding behaviour of ducks reflects a number of conflicts, both between and within the sexes. While unpaired (single) birds attempt to obtain mates, already mated males may pursue the conflicting strategies of mate guarding and extra-pair courtship or copulation in order to sequester the mate while pursuing mating opportunities outside the pair bond. If females pursue the same strategies pair members will also be in conflict. We have sought to understand the nature of these complex interactions in the Harlequin Duck (Histrionicus histionicus), and in the present paper examine the conflict between paired and unpaired birds as it is manifest in agonistic encounters. Pairs are predicted by game theory models to dominate single males as a result of one or more competitive asymmetries and this prediction was supported, pairs both initiating and winning encounters against single males. Compared to pairs, single males were more likely to retreat and less likely to display back to an initiating display. Similarly, individuals were less likely to retreat in response to single male displays than to those of paired males or females. Displays in the order 'head nod away', 'head nod at' and 'extended neck' were increasingly likely to result in a win. Responding birds tended to match the initiator's display and males showed gradual escalation in their own displays. The greater use of 'extended neck' by females probably reflected its use for inciting. Single males used more high intensity display (extended neck) and less low intensity display (head nod) against other single males than against pairs, in accord with the game theory prediction that encounters between closely-matched opponents will be of higher intensity. As a* *consequence of the dominance of pairs over single males the latter may find it impossible to obtain a mate on the breeding ground. This dominance, together with close mate guarding by both sexes, and female fidelity, is responsible for the rarity or absence of extra-pair copulations and mate switching, and the consequent strict monogamy found in this species.*

**Key Words: Harlequin Duck, breeding status, aggressive interactions, aggressive displays, mate guarding.**

Social interactions between ducks in the breeding season have long been of interest, posing questions concerning the reproductive strategies of males and females, and the function and meaning of displays in furthering reproductive goals (McKinney 1992). These questions are also of general importance to behavioural ecologists interested in communication and the evolution of competitive and sexual strategies.

The Anatidae are a largely socially monogamous group in which mate guarding by the male is strongly developed (McKinney 1986). While unpaired birds attempt to obtain mates, already mated males may pursue the conflicting strategies of mate guarding and extra-pair courtship or copulation in order to sequester the mate while pursuing mating opportunities outside the pair bond (Anderson & Titman 1992; Birkhead & Møller 1992; McKinney & Evarts 1998). Females of some birds species also seek extra-pair copulations (EPCs: Birkhead & Møller 1992) and guard their mates by aggression against other females (McKinney *et al.* 1978; Stolen & McKinney 1983; Hurly & Robertson 1984; McKinney 1985; Gowaty 1996; Sandell 1998), by soliciting copulation from the mate (Stolen & McKinney 1983; Petrie 1992; Hunter *et al.* 1993; Eens & Pinxten 1995, 1996) and perhaps by threatening cuckoldry (Petrie & Kempenaers 1998). Female mate guarding could function to avoid desertion (and loss of paternal care in some taxa), to prevent sperm depletion, or to reduce the risk of disease or parasite transmission consequent on the mate's copulation with another female (Petrie 1992; Hunter *et al.* 1993; Petrie & Kempenaers 1998).

We have sought to understand the nature of these interactions in the Harlequin Duck *Histrionicus histrionicus.* In a related study (Lazarus, Inglis & Torrance, submitted) field experiments were used with model birds in order to understand how the strategies of mate guarding and extra-pair courtship are employed and signalled in this species. It was found that both sexes mate guarded by intervening between the mate and the competitor, and by signalling with the *head nod* display. Single (unpaired) and paired males also used this display to signal extra-pair courtship or intention to copulate. The male and female of a pair may therefore be in conflict, one or both seeking extra-pair copulations or a new mate and the partner attempting to prevent infidelity by guarding and by aggression to sexual competitors. A single interaction between breeding pairs might therefore involve both agonistic and courtship signals, directed at either the mate or extra-pair individuals. Although the existence of these conflicts of interest is now appreciated (Petrie & Kempenaers 1998; Smith & Sandell 1998), the behavioural routes to their resolution remain largely unexplored, both theoretically and empirically. Our experiments with model birds addressed the nature and outcome of these conflicts.

Throughout its breeding range in Eastern Siberia, North America, Greenland and Iceland the Harlequin Duck breeds only on turbulent streams and rivers and winters on coastal waters. Pairing occurs early in the winter (Gowans *et al.* 1997) and paired individuals remain close together continuously until egg-laying, at which time the male abandons his mate, providing no parental care (Bengtson 1966). Pairs often reunite in successive seasons (Bengtson 1972; Gowans *et al.* 1997; Robertson *et al.* 1998). Mate guarding by the male is close and continuous and, although interactions between pairs - and between pairs and unpaired males - are frequent, extra-pair copulation and mate switching are either rare or absent (Inglis *et al.* 1989). Experiments with models (Lazarus, Inglis & Torrance, submitted) revealed that females also mate guard. The *head nod* - a forward elliptical movement of the head and neck - is the major agonistic and sexual display, and is used by both sexes. Males *head nod* in courtship, and before and after copulation, and females *head nod* at their mate to incite him to attack other males (Inglis *et al.* 1989; Lazarus, Inglis & Torrance submitted; Gowans *et al.* 1997). Inglis *et al.* (1989) illustrate the form of the display with a series of photographs.

In the present paper the effect of sex and breeding status (paired females, paired males and unpaired males) were examined in relation to the outcome of these mate guarding/courtship interactions in the Harlequin Duck, concentrating on their agonistic function. It was predicted that interactions between pairs and unpaired males will tend to result in wins for the pairs due to one or more of the following contest asymmetries favouring pairs that emerge from games theory analyses of the evolution of aggressive behaviour (Maynard Smith & Parker 1976; Leimar & Enquist 1984; Enquist & Leimar 1987). First, paired males may win as a result of the uncorrelated asymmetry of 'ownership' of a female that they enjoy, which is predicted to result in conventional withdrawal by the intruder. Second, as a consequence of male-male competition or mate choice, paired males may have greater resource holding power (RHP: Parker 1974) than unpaired males (as in American Wigeon, *Anas americana:* Wishart 1983), and tend to win encounters as a result. Even if this is not so, the combined RHP of paired male and female are likely to outweigh that of a single unpaired male. This 'unit size' advantage is seen in geese (Boyd 1953; Black & Owen 1989). Third, the net benefit of a win for a paired male will be greater if an unpaired male must invest courtship in a newly acquired female, costs that have already been paid by the paired male (Parker 1974; Ewald & Rohwer 1980). Wins by paired males over single males would then be predicted as a consequence of the greater benefit of the win for the former.

In addition to testing the hypothesis that pairs will dominate single males, how the asymmetries between them are expressed in the detailed course of agonistic encounters was examined, and in doing so more general aspects of the nature of such encounters were addressed.

## Methods

The study was conducted in May and June of 1978 and 1980, before nesting began, in northern Iceland on the Laxá River, about 6km downstream of its exit from Lake Mývatn. The species is not territorial on our study site, where population density is high (Bengtson 1972; Inglis *et al.* 1989). Further details of the study site, and of the breeding behaviour, postures and displays of the Harlequin Duck are described by Bengtson (1966, 1972) and Inglis *et al.* (1989).

Birds were observed through telescopes from two hides erected on hillsides overlooking the river and recorded agonistic interactions opportunistically using audio and video recorders. Individuals were monitored from the onset of an interaction until they moved out of sight, until the interaction ceased, or until too many birds became involved for recording to be reliable.

For the purposes of analysis an agonistic interaction involved the 'initiator(s)' who gave the first display and the 'receiver(s)' of that display. Initiator(s) and receiver(s) might then exchange further displays until one side retreated or until both sides stopped displaying without a retreat by either. In the former case a 'win' was recorded for the individual(s) that stayed and a 'loss' for those that retreated. In the latter case a 'draw' was recorded. We recorded the sex and breeding status (paired or unpaired) of initiator and receiver and at least the first display or response of each party (see below). Analysis of cause and effect beyond the first two exchanges of an interaction becomes difficult without a great amount of data, and was not attempted. Since members of a pair maintain continuous and close proximity to each other (Inglis *et al.* 1989) paired and single males could be readily distinguished. There were approximately twice as many pairs as single males on the study area (Inglis *et al.* 1989). Unpaired females were rare, being seen on only three occasions.

First 'responses' by the receiver were classified as: display, stay without displaying or retreat. The displays recorded were *head nod at*, *head nod away* and *extended neck* (Inglis *et al.* 1989). The *head nod* is made in line with the long axis of the body but the angle between a *head nodding* bird and the receiver of the display varied. If the *head nod* was directed at a point within 45 degrees each side of the receiver, the display was termed *head nod at*; otherwise it was termed *head nod away*. During an interaction the *head nod* often became more rapid and vigorous with the long axis of the ellipse shifting increasingly toward the horizontal. The orientation would also change so that the beak was pointed more directly at the receiver. At this point another display, the *extended neck* (Inglis *et al.* 1989) was commonly seen. In this display the neck and head of the displaying duck are stiffly extended horizontally toward the other bird(s). The display was often followed by the bird running or swimming rapidly towards the other bird(s); the *rush*.

The proportion of encounters that included the different responses and displays was analysed using general linear models (GLIM 1987, version 3.77), employing a logistic model with a Poisson error distribution. The $\chi^2$ and $P$ values reported are derived from this analysis, unless otherwise stated. All tests are two-tailed. It is not known to what extent the same birds were sampled in different encounters. Population size in the study area was about 50 pairs and 25 unpaired males (Bengtson 1972; Gardarsson 1979; Inglis *et al.* 1989) and these birds were not sedentary but moved daily through the study area on their way to and from the roosting sites (Inglis *et al.* 1989), thus increasing the likely number of different individuals that were sampled in the study. In addition, psuedoreplication is unlikely to be a serious problem for our conclusions since most of the effects reported are significant at $P<0.001$ and a number of independent tests point to the same general conclusion concerning status effects.

## Results

To put the results in a time budget context, systematic scan data showed that 5.4% of the day was spent by paired males in agonistic encounters, which was significantly more than both the 2.7% spent by paired females and the 1.8% by single males (see Inglis *et al.* 1989 for further details of methods).

### Influence of breeding status on encounter initiation and outcome

To determine the influence of breeding status on the initiation and outcome of agonistic encounters we analyzed the results of 145 complete encounters using three factors in a GLIM analysis: status of initiator and receiver (pair or single male), and encounter outcome (win, draw or lose defined as above).

The initiator was more likely to win an encounter (62%) than to draw (25%) or lose (13%) ($\chi^2$= 55.2, df = 2, $P<0.001$), and status significantly influenced this effect. Thus 65% of pairs won encounters they initiated compared with 48% for single males ($\chi^2$= 7.0, df=2, $P<0.05$). Similarly 20% of pairs won encounters in which they were the receivers, compared with only 9% of single males ($\chi^2$= 8.4, df=2, $P<0.02$).

Pairs initiated 90% of the 92 encounters between pairs and single males, and of the 71 (77%) of these encounters that had a winner, 89% were won by pairs. These proportions are both significantly greater than equality between the two status categories (Binomial tests, corrected for continuity, both $P<0.00006$).

### Influence of initiator's display on receiver's response and encounter outcome

Data from 229 encounters were examined to determine the influence of status, and the type of display used to initiate an encounter, upon the first response of the receiver (which also decided the encounter outcome if the response was to retreat). Four factors were used in a GLIM analysis: status of initiator (paired male, paired female, single male) and receiver (pairs and single males), first display of initiator (*head nod away, head nod at* or *extended neck*) and first response of receiver (display, stay without displaying or retreat). As there were very few initiations by single males towards other single males and by paired females against pairs, it was necessary to conduct two analyses with the contingency table collapsed over each of the two status factors in turn. The effect of different initiator displays on the receiver's response is described first, so that conclusions can be drawn about the relative effectiveness of the three displays in winning encounters. This information is then used, in the following section, to illuminate the effects of status on the use of the various displays.

The influence of initiator display on receiver response was analysed by collapsing the data across the receiver status factor, as described above. Initiator displays in the order *head nod away, head nod at* and *extended neck* were increasingly likely to be followed by the receiver retreating, and decreasingly likely to be followed by the receiver ignoring or displaying back ($\chi^2$=110.2, df=4, $P$<0.001, **Figure 1**). This trend was shown for every combination of initiator and receiver status category (except that pairs never retreated to an initiating single male, whatever its display). We therefore place the displays *head nod away*, *head nod at* and *extended neck*, respectively, on a scale of increasing 'intensity', defined in terms of consequent probability of success in winning an encounter. We refer to a transition (within or between individuals) from a lower to a higher intensity display as 'escalation'.

For the 83 encounters in which the receiver displayed back (pooled over the status categories of both initiator and receiver) we examined the effect of the type of display used by the initiator on the display response of the receiver. There was a significant interaction between the two, the receiver tending to match the display used to initiate the encounter, particularly for the lowest intensity display, *head nod away* ($\chi^2$=11.4, df=4, $P$<0.05; **Figure 2**).

Paired and single males escalated gradually from their own first display in an encounter (sometimes with intervening displays by the other party). Thus, an initial *head nod at* was more likely to be followed by *extended neck* (probability=0.27) than

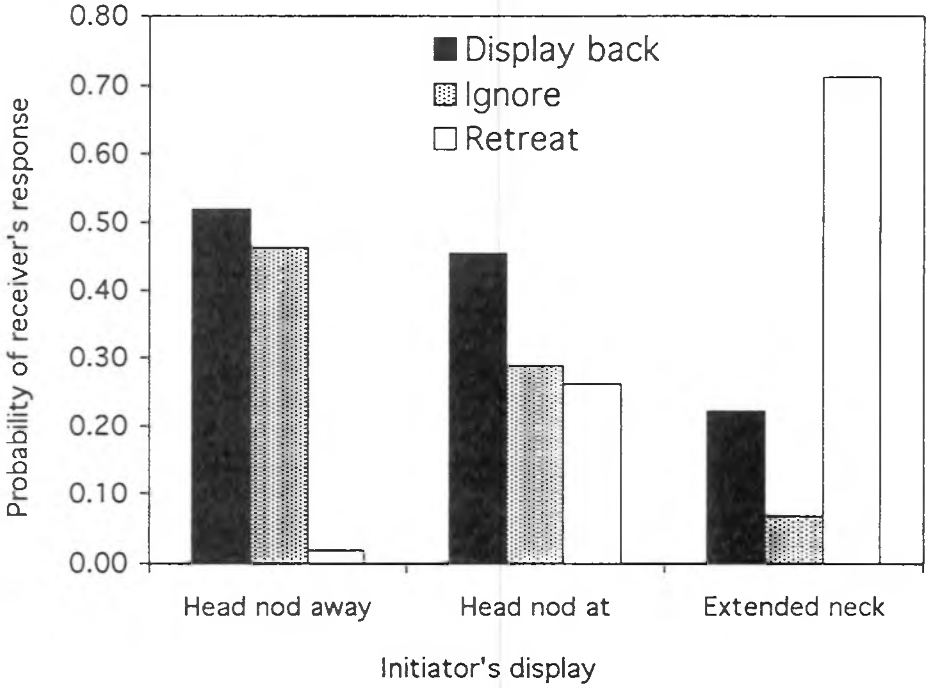

**Figure 1**. Influence of the initiator's display on the receiver's response. Sample sizes: *head nod away* = 52; *head nod at* = 72; *extended neck* = 104.

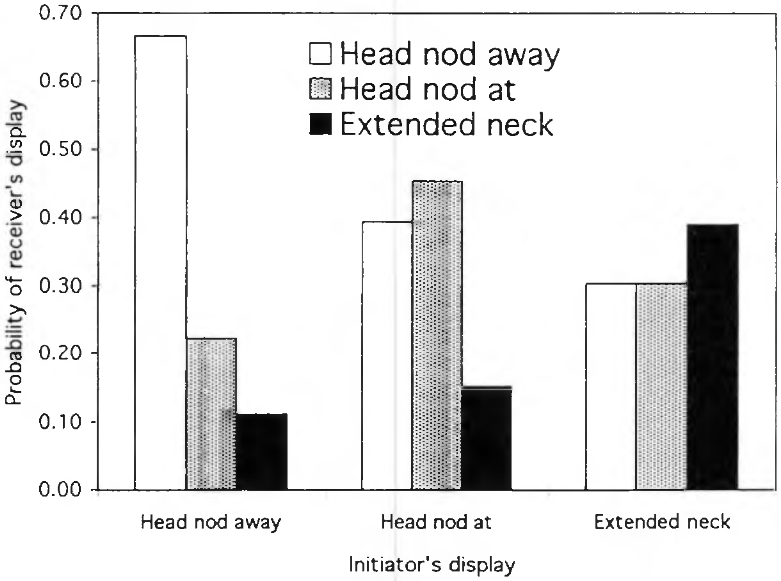

**Figure 2.** Influence of the initiator's display on the receiver's display, in those encounters when the receiver displayed back. Sample sizes: *head nod away* = 27; *head nod at* = 33; *extended neck* = 23.

an initial *head nod away* was to be followed by *extended neck* (probability=0.04; chi square test corrected for continuity, $\chi^2$=12.8, df=1, $P$<0.0004, n=171 encounters). Corresponding probabilities for females were 0.29 and 0.00, respectively, a non-significant difference (Fisher's Exact Test, $P$=0.07, n=36 encounters). However, since females rarely showed *head nod away* as their first display (**Figure 3**), and consequently the sample size of *head nod away* for this analysis was small, any conclusion about gradual escalation of display in females remains uncertain.

## Influence of status on display and encounter outcome

The four status effects examined were the influence of initiator status on initiator and receiver display, and the influence of receiver status on initiator and receiver display. In the first analysis, data were collapsed across the receiver status factor and initiator status effects were examined. Paired males initiated 60% of the interactions compared with 23% for paired females and 17% for single males, whereas the expected figures are 30%, 30% and 40% respectively. Thus paired males initiated far more encounters than expected and single males far fewer ($\chi^2$=74.4, df=2, $P$<0.001).

The initiator's status influenced the type of display it employed ($\chi^2$=25.4, df=4, $P$<0.001). Males, whether paired or single, used the two orientations of *head nod* and *extended neck* equally, whilst females largely used the high intensity *extended neck* and rarely *head nod away* (**Figure 3**). Independent of the initiating display, the receiver's response was influenced by the initiator's status. Receivers were more likely to display back and less likely to

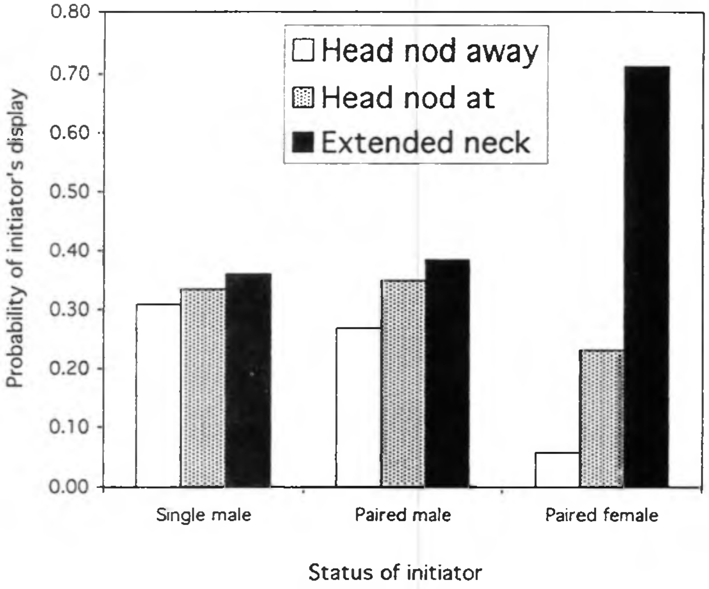

**Figure 3**. Influence of the status of the initiator on its first display in the encounter. Sample sizes: single male = 39; paired male = 138; paired female = 52.

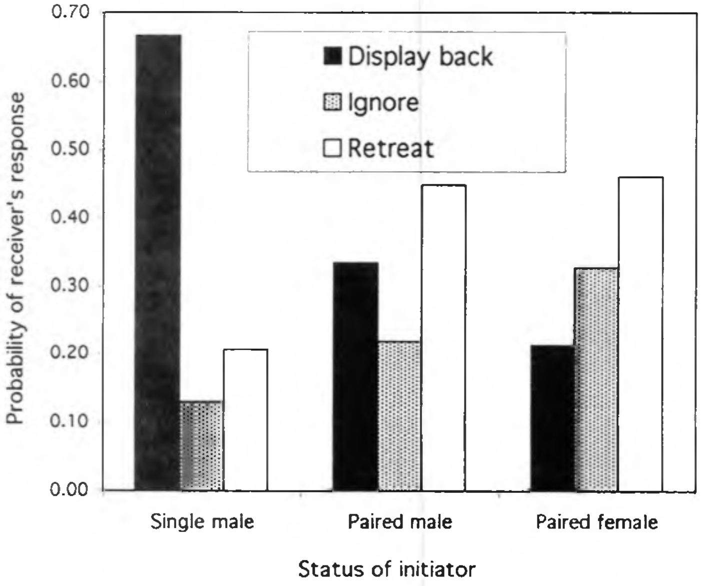

**Figure 4**. Influence of the status of the initiator on the receiver's response. Sample sizes: single male = 39; paired male = 138; paired female = 52.

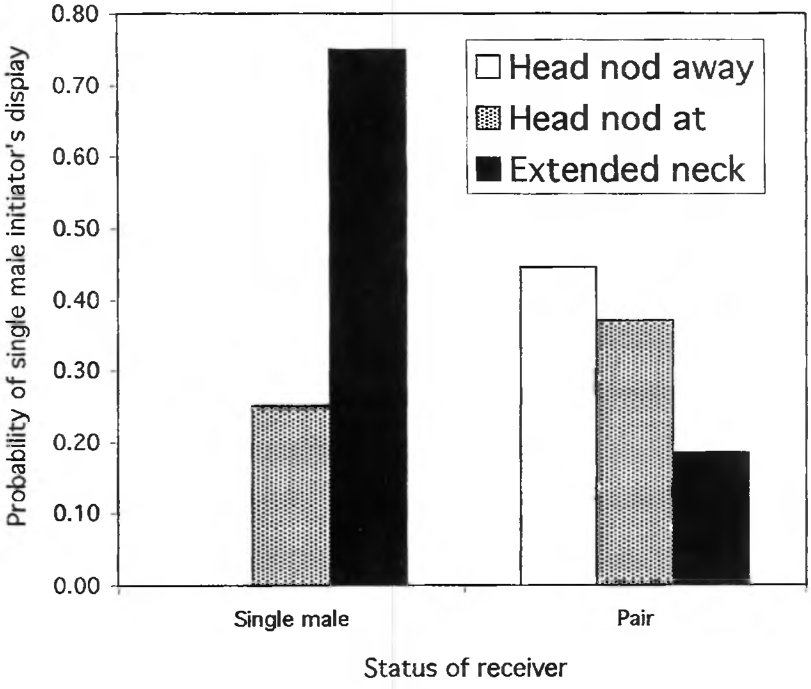

**Figure 5**. Influence of the status of the receiver on the first display of an initiating single male. Sample sizes: single male = 12; pair = 27. The probability value of *head nod away* to a single male receiver is zero.

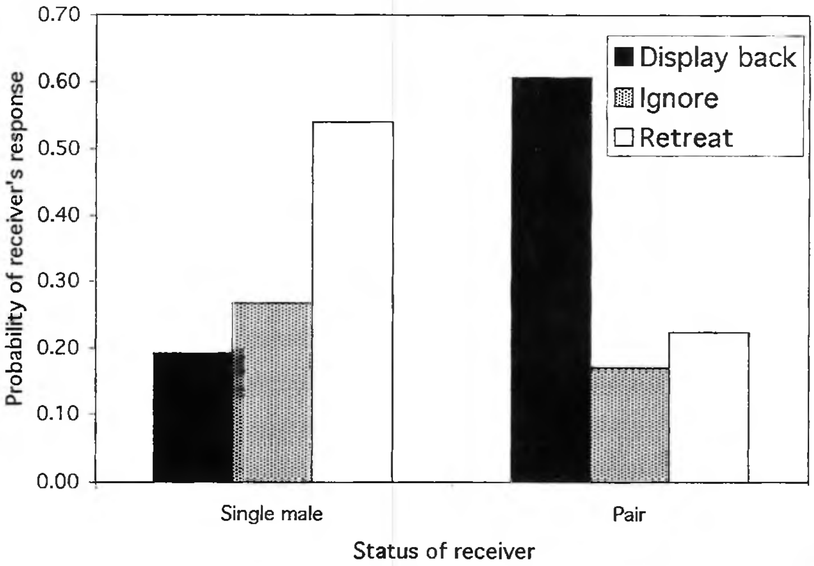

**Figure 6**. Influence of the status of the receiver on its own response. Sample sizes: single male = 135; pair = 94.

ignore or retreat from a display by a single male than they were to displays from paired males or paired females ($\chi^2$=20.9, df=4, $P$<0.001, **Figure 4**). The interaction between all three factors (initiator status, initiator display, receiver response) was not significant.

In the second analysis, data were collapsed across the initiator status factor and receiver status effects were examined. Receiver status influenced the type of display used to initiate an encounter: the high intensity *extended neck* was used more frequently, and the low intensity *head nod away* less frequently against single males than against pairs ($\chi^2$=14.5, df=2, $P$<0.001). However, when examining this relationship for each initiator status separately (for *extended neck* versus *head nod*, since sample sizes did not allow separation of the two orientations of *head nod* in the analysis) it held only for single males ($\chi^2$=11.5, df=1, $P$=0.0007, **Figure 5**). Paired male and female initiators displayed similarly to both single males and pairs. The receiver's status also affected its response; single males were more likely to retreat and less likely to display back than members of pairs ($\chi^2$=13.1, df=2, $P$<0.01, **Figure 6**). This was the case in response to both single and paired male initiators, but not to female initiators. The interaction between all three factors (receiver status, initiator display, receiver response) was not significant.

## Discussion

### Influence of status on the initiation and outcome of encounters

Initiators of encounters tended to win them, as is commonly the case (e.g. Boyd 1953; Lazarus & Inglis 1978; Paton & Caryl 1986) and pairs initiated encounters against single males. Higher RHP individuals are more likely to initiate contests in a number of species (see Lazarus 1982, for examples) and this may explain these results since paired males may well have a higher RHP than single males (see Introduction). Alternatively, the other putative contest asymmetries between single and paired males described in the Introduction might explain these results.

We predicted that pairs will dominate single males in agonistic encounters due to one or more of these contest asymmetries. The results support this prediction, although we are not able to conclude which asymmetries are applicable to the Harlequin. First, pairs won encounters against single males. Second, as receivers, single males were more likely to retreat and less likely to display back, than pairs. Third, receivers as a whole were more likely to display back, and less likely to ignore or retreat, to single male initiators than to paired males or females.

### Display matching, escalation, orientation and encounter outcome

Initiator displays in the order *head nod away*, *head nod at* and *extended neck* were increasingly likely to result in a win, and are consequently placed on a scale of increasing 'intensity'. Although evolutionary theory, and findings, on the information content and honesty of agonistic displays has been a matter of contention (Dawkins & Krebs 1978; Caryl 1979, 1982; Hinde 1981; Krebs & Dawkins 1984; Paton & Caryl 1986; Harper 1991), Enquist (1985) has shown that selection can favour the signalling of aggressive intentions. In line with Enquist's models a number of avian studies have found evidence of a range of display types that differ consistently in their effectiveness at eliciting retreat in the opponent, as found here (e.g. Boyd 1953; Dunham 1966; Andersson 1976; Bossema & Burgler 1980). The effectiveness of the horizontal head and neck position of *extended neck* is shared by some species (e.g. Galusha & Stout 1977; Amlaner & Stout 1978) but not others (Popp 1987). The greater effectiveness of facing compared to other orientations of the same display, reported here, may be a more general phenomenon (e.g. Hayward *et al.* 1977; Paton 1986). The importance of orientation lies partly in the fact that the address (i.e. intended recipient) of a facing signal is particularly clear (Paton 1986). When three or four birds are involved in an interaction the address of *head nods* may be ambiguous to the interactants; *head nod away*, defined here in terms of orientation to the opponent, might sometimes have simultaneously been *head not at* directed at the mate. A full understanding of the meaning of display orientation requires knowledge of the position of all interactants with respect to the display. Orientation is also important in the displays of male ducks to females, again indicating the identity of the intended receiver, attracting her attention and indicating interest in her (Simmons & Weidmann 1973; McKinney 1975, 1992; Davis 1997).

When receivers displayed back they tended to match the initiator's display and males escalated the intensity of their own displays gradually. Gradual escalation during agonistic encounters, within and between contestants, is common in other species at a coarse level of analysis, and matching or gradual escalation is also found at the level of single transitions between actions (Maynard Smith & Riechert 1984; Popp 1987). However, the detailed course of interactions is often more complex than this, deescalation tending to occur in eventual losers, for example (Enquist & Jakobsson 1986; Huntingford & Turner 1987; Popp 1987). Our findings on matching and gradual escalation apply only to the very first actions and responses in an encounter.

### Influence of status on the use of displays

In initiating encounters, females mainly used the high intensity *extended neck*, while males (paired and unpaired) used *extended neck* and the two *head nod* orientations equally. The greater use of *extended neck* by females probably reflects, at least partly, its use for inciting, since *extended neck* inciting movements precede *head nod at* by the female to her mate (Inglis *et al.* 1989). These initial *extended necks* by females may incite further display by the mate, which in turn increases the pair's chance of winning the encounter. This raises the general issue of whether the relationship between the initial display and the result of the encounter is a causal one. The relationship between initial display type and the probability of retreat by the receiver is almost certainly causal since display and retreat are the very first (and only) components of the interaction. Similarly, the relationship between initial display type and the probability of ignoring or displaying back is also likely to be causal, but here the ultimate outcome of the encounter is unknown. Inciting is an example of the more general phenomenon of female influences on male display in wildfowl (Weidmann & Darley 1971; Hausberger & Black 1990).

Single male initiators used more high intensity display (*extended neck*) and less low intensity display (*head nod*) against other single males than against pairs. In line with game theory prediction (Maynard

Smith & Parker 1976), others also report that more closely-matched opponents have higher intensity encounters (e.g. Lazarus 1982; Enquist & Jakobsson 1986; Turner & Huntingford 1986).

## Conclusion

In analysing use of the *head nod* we have concentrated on its agonistic function. However, the *head nod* is a multifunctional signal (see also McKinney *et al.* 1990; McKinney 1992; Davis 1997) used also in courtship, in copulation sequences, and in female inciting (Inglis *et al.* 1989; Gowans *et al.* 1997), and our model experiments address the multifunctional property of the display (Lazarus, Inglis & Torrance submitted).

Whichever asymmetries are responsible for the dominance of pairs over single males the consequence is that unpaired males on the breeding ground find it difficult, perhaps impossible, to obtain a mate. This dominance, together with close mate guarding by both sexes, and female fidelity (Inglis *et al.* 1989, Lazarus, Inglis & Torrance submitted) is responsible for the rarity or absence of EPCs and mate switching in Harlequin Ducks (Inglis *et al.* 1989), and the consequent strict monogamy found in this species.

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## References

Amlaner Jr., C.J. & Stout, J.F. (1978). Aggressive communication by *Larus glaucescens* part VI: Interactions of territory residents with a remotely controlled, locomotory model. *Behaviour* **66**: 223-251.

Anderson, M.G. & Titman, R.D. (1992). Spacing patterns. In: Batt, B.D.J. *et al.* (Eds.). *Ecology and Management of Breeding Waterfowl.* University of Minnesota Press, Minneapolis, pp 251-289.

Andersson, M. (1976). Social behaviour and communication in the Great Skua. *Behaviour* **58**: 40-77.

Bengtson, S-A. (1966). Field studies on the Harlequin Duck in Iceland. *Wildfowl Trust Annual Report* **17**: 79-94.

Bengtson, S-A. (1972). Breeding ecology of the Harlequin Duck *Histrionicus histrionicus* (L.) in Iceland. *Ornis Scandinavica* **3**: 1-19.

Birkhead, T.R. & Møller, A.P. (1992). *Sperm Competition: Evolutionary Causes and Consequences.* Academic Press, London.

Black, J.M. & Owen, M. (1989). Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Animal Behaviour* **37**: 199-209.

Bossema, I. & Burgler, R.R. (1980). Communication during monocular and binocular looking in European jays. *Behaviour* **74**:274-283.

Boyd, H. (1953). On encounters between wild White-fronted Geese in winter flocks. *Behaviour* **5**:85-129.

Caryl, P.G. (1979). Communication by agonistic displays: what can games theory contribute to ethology? *Behaviour* **68**:136-169.

Caryl, P.G. (1982). Animal signals: a reply to Hinde. *Animal Behaviour.* **30**: 240-244.

Davis, E.S. (1997). The Down-Up display of the Mallard: one display, two orientations. *Animal Behaviour* **53**: 1025-1034.

Dawkins, R. & Krebs, J.R. (1978). Animal signals: information or manipulation? In: Krebs, J.R. & Davies, N.B. (Eds.). *Behavioural Ecology: An Evolutionary Approach,* 1st edn. Blackwell Scientific Publications, Oxford, pp 282-309.

Dunham, D.W. (1966). Agonistic behavior in captive Rose-breasted Grosbeaks, *Pheucticus ludovicianus* (L.). *Behaviour* **27**: 160-173.

Eens, M. & Pinxten, R. (1995). Inter-sexual conflicts over copulations in the European Starling: evidence for the female mate-guarding hypothesis. *Behavioural Ecology and Sociobiology.* **36**: 71-81.

Eens, M. & Pinxten, R. (1996). Female European Starlings increase their copulation solicitation rate when faced with the risk of polygyny. *Animal Behaviour* **51**: 1141-1147.

Enquist, M. (1985). Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour* **33**: 1152-1161.

Enquist, M. & Jakobsson, S. (1986). Decision making and assessment in the fighting behaviour of *Nanacara anomala* (Cichlidae, Pisces). *Ethology* **72**: 143-153.

Enquist, M. & Leimar, O. (1987). Evolution of fighting behaviour: the effect of variation in resource value. *Journal of Theoretical Biology* **127**: 187-205.

Ewald, P.W. & Rohwer, S. (1980). Age, coloration and dominance in non-breeding hummingbirds: a test of the asymmetry hypothesis. *Behavioural Ecology and Sociobiology.* **7**: 273-279.

Galusha, J.G. & Stout, J.F. (1977). Aggressive communication by *Larus glaucescens* part IV: Experiments on visual communication. *Behaviour* **62**: 222-235.

Gardarsson, A. (1979). Waterfowl populations of Lake Mývatn and recent changes in numbers and food habits. *Oikos* **32**: 250-270.

GLIM. (1987). *The Generalised Linear Interactive Modelling System.* Numerical Algorithms Group. Nuffield Press, Oxford.

Gowans, B., Robertson, G.J. & Cooke, F. (1997). Behaviour and chronology of pair formation by Harlequin Ducks *Histrionicus histrionicus*. *Wildfowl* **48**: 135-146.

Gowaty, P.A. (1996). Battles of the sexes and origins of monogamy. In: Black, J.M. (Ed.). *Partnerships in Birds: The Study of Monogamy.* Oxford University Press, Oxford, pp 21-52.

Harper, D.G.C. (1991). Communication. In: Krebs, J.R. & Davies, N.B. (Eds.). *Behavioural Ecology: An Evolutionary Approach*, 3rd edn. Blackwell Scientific Publications, Oxford, pp 374-397.

Hausberger, M. & Black, J.M. (1990). Do females turn males on and off in Barnacle Goose social display? *Ethology* **84**: 232-238.

Hayward Jr., J.L., Gillett, W.H. & Stout, J.F. (1977). Aggressive communication by *Larus glaucescens* part V: orientation and sequences of behaviour. *Behaviour* **62**: 236-276.

Hinde, R.A. (1981). Animal signals: ethological and games-theory approaches are not incompatible. *Animal Behaviour* **29**: 535-542.

Hunter, F.M., Petrie, M., Otronen, M., Birkhead, T. & Møller, A.P. (1993). Why do females copulate repeatedly with one male? *Trends in Ecology and Evolution* **8**: 21-26.

Huntingford, F.A. & Turner, A.K. (1987). *Animal Conflict.* Chapman and Hall, London.

Hurly, T.A. & Robertson, R.J. (1984). Aggressive and territorial behaviour in female Red-winged Blackbirds. *Canadian Journal of Zoology* **62**: 148-153.

Inglis, I.R., Lazarus, J. & Torrance, R. (1989). The pre-nesting behaviour and time budget of the Harlequin Duck *Histrionicus histrionicus*. *Wildfowl* **40**: 55-73.

Krebs, J.R. & Dawkins, R. (1984). Animal signals: mind-reading and manipulation. In: Krebs, J.R. & Davies, N.B. (Eds.). *Behavioural Ecology: An Evolutionary Approach*, 2nd edn. Blackwell Scientific Publications, Oxford, pp 380-402.

Lazarus, J. (1982). Competition and conflict in animals. In: Colman, A.M. (Ed.). *Cooperation and Competition in Humans and Animals*. Van Nostrand Reinhold, Wokingham, pp 26-56.

Lazarus, J. & Inglis, I.R. (1978). Breeding behaviour of the Pink-footed Goose: parental care and vigilant behaviour during the fledging period. *Behaviour* **65**: 62-88.

Leimar, O. & Enquist, M. (1984). Effects of asymmetries in owner-intruder conflicts. *Journal of Theoretical Biology* **111**: 475-491.

Maynard Smith, J. & Parker, G.A. (1976). The logic of asymmetric contests. *Animal Behaviour* **24**: 159-175.

Maynard Smith, J. & Riechert, S.E. (1984). A conflicting-tendency model of spider agonistic behaviour: Hybrid-pure population line comparisons. *Animal Behaviour* **32**: 564-578.

McKinney, F. (1975). The evolution of duck displays. In: Baerends, G., Beer, C. & Manning, A. (Eds.). *Function and Evolution in Behaviour: Essays in Honour of Professor Niko Tinbergen, F.R.S.* Clarendon Press, Oxford, pp 331-357.

McKinney, F. (1985). Primary and secondary male reproductive strategies of dabbling ducks. In: Gowaty, P.A. & Mock, D.W. (Eds.). *Avian Monogamy. Ornithological Monographs* **37**: 68-82.

McKinney, F. (1986). Ecological factors influencing the social systems of migratory dabbling ducks. In: Rubenstein, D.I. & Wrangham, R.W. (Eds.). *Ecological Aspects of Social Evolution*. Princeton University Press, Princeton, pp 153-171.

McKinney, F. (1992). Courtship, pair formation, and signal systems. In: Batt, B.D.J. *et al.* (eds.). *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press, Minneapolis, pp 214-250.

McKinney, F. & Evarts, S. (1998). Sexual coercion in waterfowl and other birds. In: Parker, P.G. & Burley, N.T. (Eds.). *Avian Reproductive Tactics: Female and Male Perspectives. Ornithological Monographs* **49**: 163-195.

McKinney, F., Siegfried, W. R., Ball, I. J. & Frost, P. G. H. (1978). Behavioural specializations for river life in the African black duck. *Zeitschrift fur Tierpsychologie* **48**: 349-400.

McKinney, F., Sorenson, L. G. & Hart, M. (1990). Multiple functions of courtship displays in dabbling ducks (*Anatini*). *Auk* **107**:188-191.

Parker, G.A. (1974). Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology* **47**: 223-243.

Paton, D. & Caryl, P.G. (1986). Communication by agonistic displays: I. Variation in information-content between samples. *Behaviour* **98**: 213-239.

Paton, D. (1986). Communication by agonistic displays: II. Perceived information and the definition of agonistic displays. *Behaviour* **99**: 157-175.

Petrie, M. (1992). Copulation frequency in birds: why do females copulate more than once with the same male? *Animal Behaviour* **44**: 790-792.

Petrie, M. & Kempenaers, B. (1998). Extra-pair paternity in birds: explaining variation between species and populations. *Trends in Ecology and Evolution* **13**: 52-58.

Popp, J.W. (1987). Agonistic communication among wintering Purple Finches. *Wilson Bulletin* **99**: 97-100.

Robertson, G. J., Cooke, F., Goudie, R. I. & Boyd, W. S. (1998). The timing of pair formation in Harlequin Ducks. *Condor* **100**: 551-555.

Sandell, M. I. (1998). Female aggression and the maintenance of monogamy: female behaviour predicts male mating status in European starlings. *Proceedings of the Royal Society, London B* **265**: 1307-1311.

Simmons, K.E.L. & Weidmann, U. (1973). Directional bias as a component of social behaviour with special reference to the Mallard, *Anas platyrhynchos*. *Journal of Zoology, London* **170**: 49-62.

Smith, H. G. & Sandell, M. I. (1998). Intersexual competition in a polygynous mating system. *Oikos* **83**: 484-495.

Stolen, P. & McKinney, F. (1983). Bigamous behaviour of captive Cape Teal. *Wildfowl* **34**: 10-13.

Turner, G.F. & Huntingford, F.A. (1986). A problem for game theory analysis: assessment and intention in male mouthbrooder contests. *Animal Behaviour* **34**: 961-970.

Weidmann, U. & Darley, J. (1971). The role of the female in the social display of Mallards. *Animal Behaviour* **19**: 287-298.

Wishart, R.A. (1983). Pairing chronology and mate selection in the American Wigeon *Anas americana*. *Canadian Journal of Zoology*. **61**: 1733-1743.