MATE GUARDING CONFLICT, EXTRA-PAIR COURTSHIP AND SIGNALLING IN THE HARLEQUIN DUCK, HISTRIONICUS HISTRIONICUS

by

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Summary

Socially monogamous birds pursuing extra-pair reproductive strategies may be in conflict, both sexes seeking new mates or copulations outside the pair, while simultaneously attempting to prevent infidelity by the partner. Intra-pair conflicts are augmented by inter-pair conflicts when pairs meet, when all four individuals may be sexually attracted to one member of the other pair while seeking to prevent their mate from copulating, or deserting, with the other. We studied the dynamics, signalling and resolution of these conflicts in a field experiment with the harlequin duck, recording responses to single model birds of both sexes, and to model pairs. Both sexes mate guarded by placing themselves between the mate and a model competitor, and by signalling with the head nod display. Females were closer to model pairs than their mates. Female mate guarding responded adaptively to infidelity risk, increasing to models of paired females, single females and single females inviting copulation, respectively. Males head nodded to signal the goal of (extra-pair) copulation, pairing or mate switching.

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Courtship by unpaired males increased to models of paired females, single females and single females inviting copulation, respectively. Paired males courted these models equally, perhaps inhibited by the parallel increase in mate guarding of their mates. Males signalled mate guarding using the head nod more than females, but this predicted difference in mate guarding was not shown for the measure of relative proximity to the models. In spite of male extra-pair courtship the harlequin is strictly monogamous, due to female fidelity and close mate guarding. The use of models revealed mate guarding by females, and failed extra-pair reproductive attempts by males, neither of which were apparent from observational studies alone.

Keywords: courtship signals, extra-pair courtship, harlequin duck, Histrionicus histrionicus, mate guarding, mate guarding conflict, mate guarding signals.

Introduction

It is now well understood that socially monogamous birds pursue reproductive strategies outside the pair bond. Males may pursue the conflicting strategies of mate guarding and extra-pair courtship and copulation in order to sequester the mate while pursuing mating opportunities outside the pair bond (Birkhead & Möller, 1992; McKinney & Evarts, 1998). Females also seek extra-pair copulations (EPCs: Birkhead & Möller, 1992) and guard their mates by aggression against other females (McKinney et al., 1978; Stolen & McKinney, 1983; McKinney, 1985; Sandell, 1998) and by soliciting copulation from the mate (Stolen & McKinney, 1983; Hunter et al., 1993; Eens & Pinxten, 1996). Female mate guarding functions to avoid desertion, to prevent sperm depletion or to reduce the risk of disease or parasite transmission consequent on the mate’s copulation with another female (Hunter et al., 1993; Petrie & Kempenaers, 1998).

The sexes may therefore be in conflict, one or both seeking copulations or new mates outside the pair, while simultaneously attempting to prevent infidelity by the mate. Such intra-pair conflicts will be augmented by inter-pair conflicts when pairs meet, when all four individuals might be sexually attracted to one member of the other pair while seeking to prevent their mate from copulating, or deserting, with the other. Although the existence of these conflicts of interest is now appreciated (Petrie & Kempenaers, 1998; Smith & Sandell, 1998), the nature of their resolution remains largely unexplored and raises unsolved problems in the coevolution of intra-specific signals and competing strategies.

Understanding these multiple conflicts also raises methodological problems. For example, a male signalling in the presence of his mate and another
pair might be directing his signal to the male (mate guarding), to his own mate (mate guarding or courtship), to the other female (courtship) or to any combination of these.

Our aim in this study was to explore this sexual conflict between breeding pairs, focusing on the following questions. Which of the sexes mate guards; how are mate guarding and extra-pair courtship signaled; and how does guarding respond to infidelity risk? If both sexes mate guard by attempting to place themselves between their partner and a sexual competitor, how is the resulting spatial conflict between male and female resolved? Our method was to compare the responses of birds to models of males, females and pairs. The use of models has several advantages. When members of a pair travel closely together, the use of single models of each sex provides a means of distinguishing between the influence of each member of a pair on the mate guarding and extra-pair courtship tactics of target birds, and between the signals employed for these different tactics. This would be difficult with naturalistic observations, particularly where most individuals are paired, as in our study species (see below). Stationary models also facilitate measurement of the spatial aspects of mate guarding and remove the variability in signalling that is due to the behaviour of target animals, variability that often prohibits a proper analysis of signal function (e.g. Barnard, 1990).

Our study species was the harlequin duck, *Histrionicus histrionicus* (L.), a member of the Anatidae, a largely socially monogamous group in which mate guarding by the male is strongly developed (McKinney, 1986). Pairing in the harlequin occurs early in the winter (Gowans *et al.*, 1997) and paired individuals remain together 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; Robert-son *et al.*, 1998) and unpaired females are rare on the breeding ground (Inglis *et al.*, 1989). Interactions between pairs — and between pairs and unpaired males — are frequent, and pair members stay in close and continuous contact. In the hundreds of such encounters that we observed, in some 300 person-hours of observation, a forced (pair or extra-pair) copulation, and a chase that may have involved a male and an extra-pair female away from her mate, were observed only once each (Inglis *et al.*, 1989), but definite extra-pair copulation was never observed. However, paternity analysis using molecular markers has not been carried out on this population. The head nod is used by both sexes in agonistic interactions and by males in courtship sequences
(Inglis et al., 1989, 2000; Gowans et al., 1997). This display was therefore the obvious candidate for our questions concerning the signalling of mate guarding and extra-pair courtship.

In answer to the questions posed above we predicted that both sexes would mate guard (given the benefits discussed), but that males would be more motivated to guard, due to their greater net benefit from guarding (arguments summarised in Table 1). A major additional factor favouring male guarding is that, since members of a pair are always close together, guarding and extra-pair courtship are not — as the opportunity costs in Table 1 assume — mutually incompatible, so that these opportunity costs (dearer for males) can be mitigated. Following the same reasoning we predicted more extra-pair sexual activity in males than in females (Table 1). Our observational work has shown the existence of male, but not female, mate guarding (Inglis et al., 1989).

Methods

We conducted the study on the Laxá River, about 6 km downstream of its exit from Lake Mývatn in northern Iceland. Here the population density is high and the species is not territorial. The sex ratio is male-biased, with twice as many pairs as unpaired males but almost no unpaired females (Bengtson, 1972; Inglis et al., 1989). Bengtson (1972) and Inglis et al. (1989) provide further details of the study site, and of breeding behaviour and displays.

We constructed life-sized and realistically painted fibre-glass models of male and female harlequins (a highly sexually dimorphic species) in the resting posture (‘sitting head low’), in which the neck is withdrawn and the head faces forward (see Inglis et al., 1989 for photograph of model). We also made models of females in the prone posture, assumed shortly before copulation, in which the head is stretched forward on the surface of the water. The tail of the prone model was extended horizontally, not lifted as occurs immediately before sperm transfer. We used two to three identical copies of each model type.

We conducted the experiments in three different areas of the river favoured by harlequins; each of these areas contained calm shallows where they swam, and rocks on which they rested, both close to the river bank, and all ‘model types’ (see below) were placed in all three areas. The prone female model floated (anchored to the river bed), the natural position for a female in this posture. The other models were placed on selected rocks in the river, their postures being the same as those adopted by resting birds. Thus, in all cases the posture of the models matched naturally the microhabitat in which they were placed. In a single season we observed responses to the models in one area on 15 days between May 14 and June 2; in a second area on six days between May 9 and May 22; and in a third area on the five days May 29 - June 2. Egg laying usually begins at the end of May (Bengtson, 1972).

The models were used to create five experimental conditions. These five ‘model types’ were: ‘no model’; a solitary male; a solitary female; a pair (i.e. male and female placed side by side a few cm apart, as is natural for a resting pair) and a solitary prone female.
TABLE 1. The potential benefits and costs of mate guarding and extra-pair activity to male and female harlequin. Males are predicted to enjoy a greater net benefit from both activities than females (see text and supporting references in the Introduction)

<table>
<thead>
<tr>
<th>Function</th>
<th>Mate guarding</th>
<th>Potential benefit/cost to male of male mate guarding</th>
<th>Potential benefit/cost to female of female mate guarding</th>
<th>Greater benefit/lower cost to:</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Prevent EPC by mate</td>
<td>Increases paternity</td>
<td>Maintains availability of mate’s sperm</td>
<td>Male (may be equivalent to female bias in related costs in 6 below)</td>
<td>Male</td>
</tr>
<tr>
<td>2. Prevent mate switching by mate</td>
<td>Prevents STIs</td>
<td>Prevents STIs</td>
<td>Neither?</td>
<td>Male</td>
</tr>
<tr>
<td>3. Protects mate from feeding interference</td>
<td>Maintains paternity in mate’s clutch. Remating less likely due to male-biased OSR (see text)</td>
<td>Remating more likely due to male-biased OSR (see text)</td>
<td>Male (probably outweighs female bias in related costs in 7 below)</td>
<td>Male</td>
</tr>
<tr>
<td>4. Protect mate from predators: vigilance (sexes equally vigilant: Inglis et al., 1989)</td>
<td>Female improves breeding condition; important for egg quality and maternal care</td>
<td>Male improves breeding condition. There is no paternal care</td>
<td>Male</td>
<td>Male</td>
</tr>
<tr>
<td>Function</td>
<td>Potential benefit/cost to male of extra-pair courtship and copulation</td>
<td>Potential benefit/cost to female of female extra-pair courtship and copulation</td>
<td>Greater benefit/ lower cost to:</td>
<td></td>
</tr>
<tr>
<td>-------------------------------</td>
<td>------------------------------------------------------------------------</td>
<td>---------------------------------------------------------------------------------</td>
<td>---------------------------------</td>
<td></td>
</tr>
<tr>
<td>8. EPC</td>
<td>Additional offspring outside the pair</td>
<td>Fitter offspring than by own mate</td>
<td>Male</td>
<td></td>
</tr>
</tbody>
</table>

**Costs**

<table>
<thead>
<tr>
<th>Function</th>
<th>Impact on body condition (and sperm?)</th>
<th>Impact on body condition, egg quality &amp; maternal care</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>10. Time and energy</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11. STIs</td>
<td>STIs</td>
<td>STIs</td>
<td>Neither?</td>
</tr>
<tr>
<td>12. Lost opportunity for mate guarding</td>
<td>See upper part of table for benefits of mate guarding</td>
<td>See upper part of table for benefits of mate guarding</td>
<td>Female</td>
</tr>
</tbody>
</table>

EPC-extra-pair copulation; OSR = operational sex ratio; STI = sexually transmitted infection.
The ‘no model’ condition allowed us to test for the effect of the presence of a model of each sex, since this condition presented birds with identical habitat stimuli apart from the presence of model(s). Any other kind of ‘control’ condition, such as a model of a different duck species, might itself elicit some response from the birds, so that differences between responses to such a control and to harlequin model(s) could not be interpreted as due solely to the presence of the harlequin model(s). For example, harlequins may perceive a model of a sympatric species as a competitor for a resting site, and an allopatric model as a novel object to which it might respond with fear. On each day we placed between one and four different model types simultaneously on each of a number of fixed sites in an area. For the ‘no model’ condition we used sites that at other times were occupied by resting model(s) (see above).

We used the same model types at different sites on different days to control for possible site effects, and to control for possible seasonal effects we presented the different model types on dates that were similarly distributed across the season (Kruskal-Wallis test corrected for ties, $\chi^2 = 1.9, df = 4, p = 0.75$). From a hide we observed the behaviour of pairs or single males that came within 3 m of a model site for as long as they remained within the 3 m radius (marked with boulders) and as long as no other birds came within the same area (up to a maximum of 5 minutes); we call this an ‘encounter’. Every 5 s, on an automated signal, we made an instantaneous ‘record’ of whether each bird was head nodding and, for pairs, whether the male or female was closer to the model site, or if both sexes were equidistant from it. Encounters lasting less than 30 s (6 records) were excluded from analysis.

We analysed data using general linear models analysis (GLIM, 1987, version 3.77), supplemented by Genstat for the trend analyses (Genstat 5 committee, 1993), employing a logistic model with a binomial error distribution, and the $\chi^2$ and $p$ values reported are derived from this analysis. Since many directional effects of the models were predicted a priori, and determined the experimental design, $p$ values for these effects are one-tailed. Directional predictions for other one-tailed tests are explained in the Results; otherwise two-tailed tests are used, and $\alpha = 0.05$. For each encounter GLIM calculated the probability of the relevant response per record and used each encounter as a replicate within the other factors. Thus each encounter supplied one data point to the analysis. This method weights each encounter by the number of records it contains, thus properly giving greater weight to a probability derived from a greater sample size. To calculate the probability that the set of independent statistical results for 22 encounters could have occurred under the null hypothesis that both sexes were equally close to the model pair, we used the unweighted Stouffer method for combining the results of studies (Rosenthal, 1991).

Pseudoreplication is a potential problem in field experiments with unmarked animals. We cannot quantify the degree of pseudoreplication in our study but it is unlikely that we were repeatedly testing the same few individuals. On the contrary, the following factors suggest that the proportion of our total sample that represents repeated observations on the same individuals was small. The harlequin population in the immediate study area that included our three observation areas comprised about 50 pairs and 25 unpaired males (Bengtson, 1972; Gardarsson, 1979; Inglis et al., 1989). The birds are not territorial in this area (Bengtson, 1966, 1972) and sometimes move through at least a few hundred metres of the length of the river during the day (personal observation). Each night most of the population moved out of the study area to roost (Inglis et al., 1989), and returned each morning, providing additional opportunities for population mixing. These movements within and between days therefore provided opportunities for much of the population to be exposed to the models. Birds spent about 25% of the day moving about the river rather than resting on the banks...
TABLE 2. Relative proximity of pair members to the different model types

<table>
<thead>
<tr>
<th>Model</th>
<th>Nearer member of pair</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td></td>
</tr>
<tr>
<td>No model</td>
<td>0.52 ± 0.10</td>
<td>0.42 ± 0.10</td>
<td></td>
</tr>
<tr>
<td>(N = 11)</td>
<td>0.36</td>
<td>0.60</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>0.54 ± 0.07</td>
<td>0.33 ± 0.06</td>
<td></td>
</tr>
<tr>
<td>(N = 27)</td>
<td>0.60</td>
<td>0.31</td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>0.34 ± 0.07</td>
<td>0.52 ± 0.07</td>
<td></td>
</tr>
<tr>
<td>(N = 23)</td>
<td>0.20</td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td>Pair</td>
<td>0.34 ± 0.07</td>
<td>0.54 ± 0.07</td>
<td></td>
</tr>
<tr>
<td>(N = 24)</td>
<td>0.39</td>
<td>0.54</td>
<td></td>
</tr>
<tr>
<td>Prone female</td>
<td>0.15 ± 0.04</td>
<td>0.79 ± 0.04</td>
<td></td>
</tr>
<tr>
<td>(N = 41)</td>
<td>0.16</td>
<td>0.76</td>
<td></td>
</tr>
</tbody>
</table>

Entries in each cell are, respectively: mean ± SE of the proportion of records that the male or female was nearer to the model(s), and the weighted mean of the same proportion (a single value and therefore without an SE). See text for explanation of weighted mean. N = sample size (i.e. number of encounters).

(Inglis et al., 1989) and it was only this mobile section of the population, moving about the river as described, that visited the models. While birds were on a model area others could often be seen further away on the river, and these birds often visited the model area later. On a third of the observation days we observed different birds simultaneously at two different areas. Finally, the possible magnitude of pseudoreplication is limited by the fact that the sample sizes are modest (ranging from 6 to 44; see Tables 2 and 3) and the robustness of our conclusions is strengthened by the fact that the great majority of the effects reported are significant at well below the 0.05 level. We quote mean values ± SE.

Results

Mate guarding: Relative proximity to models

We expect a mate guarding individual to attempt to place itself between its mate and its potential competitor. Since pair members were always close together (Inglis et al., 1989) an individual placing itself between the model(s) and its mate in our test areas was equivalent to that individual being the closer member of the pair to the model(s). We therefore predicted that if a particular sex was mate guarding then the presence in the ‘model type’ of a model of the same sex as the mate guarding sex (compared to its absence) would result in that sex more often being the closer member of the pair to the model type.
TABLE 3. Probability of head nodding to the different model types

<table>
<thead>
<tr>
<th>Model Status</th>
<th>Single male</th>
<th>Paired male</th>
<th>Paired female</th>
</tr>
</thead>
<tbody>
<tr>
<td>No model</td>
<td>0.000±0.000</td>
<td>0.000±0.000</td>
<td>0.000±0.000</td>
</tr>
<tr>
<td></td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>12</td>
<td>9</td>
</tr>
<tr>
<td>Male</td>
<td>0.062±0.043</td>
<td>0.045±0.016</td>
<td>0.030±0.012</td>
</tr>
<tr>
<td></td>
<td>0.044</td>
<td>0.052</td>
<td>0.028</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>24</td>
<td>24</td>
</tr>
<tr>
<td>Female</td>
<td>0.161±0.051</td>
<td>0.073±0.030</td>
<td>0.026±0.011</td>
</tr>
<tr>
<td></td>
<td>0.131</td>
<td>0.057</td>
<td>0.017</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>24</td>
<td>21</td>
</tr>
<tr>
<td>Pair</td>
<td>0.091±0.055</td>
<td>0.060±0.020</td>
<td>0.003±0.002</td>
</tr>
<tr>
<td></td>
<td>0.088</td>
<td>0.072</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>23</td>
<td>26</td>
</tr>
<tr>
<td>Prone female</td>
<td>0.134±0.038</td>
<td>0.073±0.013</td>
<td>0.021±0.007</td>
</tr>
<tr>
<td></td>
<td>0.224</td>
<td>0.065</td>
<td>0.025</td>
</tr>
<tr>
<td></td>
<td>26</td>
<td>44</td>
<td>43</td>
</tr>
</tbody>
</table>

Entries in each cell are, respectively: mean ± SE of the proportion of records that the individual was head nodding; weighted mean of the same proportion; sample size (= number of encounters). See text for explanation of weighted mean.

To test this prediction we examined the relative proximity of pair members to four model types: ‘no model’, a male, a female and a pair, using a two factor design where one factor was the presence or absence of the male model and the other factor the presence or absence of the female model. For example, ‘presence of the male model’ is represented by the model male and the model pair; while ‘absence of the male model’ is represented by the ‘no model’ condition and the female model.

Table 2 shows the mean (± SE) proportion of records (or, equivalently, the mean probability) that each sex was closer to each model type in each encounter. This table also shows the more representative ‘weighted means’ that weight each encounter by its number of records (again, excluding encounters that lasted less than 30 s); a factor that is taken into account in the GLIM analysis (see Methods). Weighted means (equivalently ‘weighted probabilities’) were calculated as the sum of records across all relevant encounters for which, say, the male was nearer, divided by the total number of records for the same encounters.
The presence of the male model doubled the weighted probability that the male would be the closer member of the pair to the model(s) from 0.25 (male model absent = no model + female mode) to 0.50 (male model present = male model + model pair) ($\chi^2_1 = 94.4$, $p < 0.0005$, one-tailed; Table 2). Correspondingly, female model presence increased the weighted probability that the female would be closer to the model(s) from 0.39 to 0.58 ($\chi^2_1 = 64.9$, $p < 0.0005$, one-tailed). The interaction between model male presence and model female presence was not significant ($\chi^2_1 = 2.3$, NS). Therefore, the effect of the presence of a model of one sex on the relative proximity of pair members to the models was independent of the presence or absence of the model of the other sex.

Each member of a pair was therefore more likely to be between its mate and the model(s) when a model of the same sex as itself was present. This confirms that the harlequins could discriminate between the male and female models and suggests that both sexes guard the mate from sexual competitors. When close to another pair the sexes may therefore be in conflict, each attempting to place itself between its partner and its same-sex competitor.

We examined putative mate guarding in the presence of a model pair by analysing the relative proximity of the male and female of a pair to this model type at the level of the individual encounter. Binomial tests were carried out separately on each encounter ($N = 22$ encounters, $\alpha = 0.05$, two-tailed). In 10 (45%) of the encounters involving pairs, the female was significantly more often closer to the models than the male, while the male was significantly more often closer in only four (18%). In the remaining eight (36%) encounters neither sex was significantly closer to the model pair. We then examined the probability that these results for the 22 encounters combined could have occurred under the null hypothesis that both sexes were equally close to the model pair (see Methods). The analysis showed that females were closer to the model pairs than the males ($z = 4.43$, $p < 0.00006$, two-tailed). In contrast, for the ‘no model’ condition the same analysis showed that neither sex was closer to the ‘model’ ($z = -0.14$, 11 encounters, $p = 0.88$, two-tailed), indicating that the result for the model pairs does not simply represent a difference in the response of each sex to the model sites themselves.

We tested the hypothesis of greater guarding motivation in males by comparing the strength of guarding of each sex against a single same sex model.
We measured strength of guarding by paired males against single male models, and by paired females against single female models, by the binomial probability values for each encounter already described. Strength of guarding against a same sex single model did not differ between the sexes (Mann-Whitney $U = 176.0$, $N_1 = 16$, $N_2 = 23$, $p = 0.42$, one-tailed).

We predicted that if paired males sought EPCs then female mate guarding, if successful, would increase progressively to the model types: a pair, a female and a prone female (i.e. guarded female, unguarded female and unguarded female inviting copulation, respectively), since they represent increasing ‘female availability’ to an extra-pair male, and therefore increasing risk of sexual competition to the female. The prediction was supported, as the weighted mean probability that the female was nearer the models pair, female and prone female, respectively, increased from 0.54 to 0.63 to 0.76 (linear trend, with Williams’ correction for excess variability in binomial data [Collett, 1991]: $\chi^2_1 = 8.3$, $p = 0.002$, one-tailed).

**Mate guarding: Signals**

We tested various hypotheses concerned with the head nod as a putative signal for mate guarding and courtship using the statistical designs already described for the analysis of proximity. Results are summarised in Table 3, which shows mean ± SE of the probability of head nodding, and weighted mean head nodding, for each model, calculated as explained for the proximity data. Head nodding was only shown in the presence of models, never in the ‘no model’ condition. While interactions between harlequin often involve the most aggressive extended neck display and outright attack (Inglis et al., 1989, 2000), such threats and attacks on the models were rare (see Discussion).

For paired birds we first checked whether model effects on nodding might work indirectly via their influence on the nodding of the partner. An influence of nodding by one of the pair on that of the other would be shown by a significant correlation of nodding probability within pairs. Calculating correlations for each model type revealed a significant correlation only for the prone female ($r = 0.35$, $N = 37$, $p = 0.035$, two-tailed).

We also found that model effects in pairs were independent of the partner’s nodding probability since there was no significant difference between model types in the slopes of the relationship between male and female nodding.
probability (scattergrams and residuals for male versus female head nodding probability showing positive linear rather than curvilinear relationships). When female nodding probability was estimated as a function of male nodding probability the 95% confidence intervals of the slopes for each model all overlapped (B coefficient ± 95% confidence intervals: male, 0.008 ± 0.337; female, 0.130 ± 0.142; pair, 0.017 ± 0.055; prone female, 0.206 ± 0.190), and the same was true for male nodding probability estimated as a function of female nodding probability (male, 0.013 ± 0.580; female, 1.242 ± 1.357; pair, 1.177 ± 3.867; prone female, 0.591 ± 0.545).

If head nodding functions as a mate guarding signal in males, directed at either the mate or the extra-pair male, then paired males should head nod more frequently than unpaired males to a male model. In an analysis of data from single males and paired males for the ‘no model’ and the male model types (Table 3) the model effect was significant, males head nodding more to a male model than to the ‘no model’ condition ($\chi^2_{1} = 26.6, p < 0.0005$, one-tailed). However, contrary to the prediction, the effect of the status of the displaying male was not significant ($\chi^2_{1} = 0.1, \text{NS}$), and neither was the interaction ($\chi^2_{1} = 0.0, \text{NS}$).

If head nodding is a mate guarding signal in females, directed either at the mate or the extra-pair female, we predict increasing female nodding to the models of a pair, a female and a prone female, respectively, due to increasing female availability and therefore increasing risk of sexual competition for the female, as argued above. As predicted there was a significant linear trend for the models pair-female-prone female ($\chi^2_{1} = 3.2$, applying Williams’ correction, $p = 0.036$, one-tailed, Table 3). Females head nodded more with model males than with no models ($\chi^2_{1} = 8.0, p < 0.01$, two-tailed, Table 3).

As predicted for a mate guarding signal (see Table 1), paired males head nodded more to single male models than paired females did to single female models ($\chi^2_{1} = 8.1, p < 0.0025$, Table 3).

Extra-pair courtship: Signals

We predicted that if head nodding is a courtship signal it will increase in males with the addition of a female model. This prediction was supported; the presence of a female model (i.e. model types: a female and a pair) as opposed to its absence (i.e. model types: ‘no model’ and a male) tripled the weighted probability of a head nod from 0.03 to 0.09 ($\chi^2_{1} = 32.0,$
p < 0.0005, one-tailed, Table 3), and equally so for both paired and single males (male status × female model presence interaction: $\chi^2_1 = 3.7$, NS, two-tailed). However, the interaction between the presence of a male model and the presence of a female model was significant ($\chi^2_1 = 23.05$, p < 0.001, two-tailed). This reflected the fact that the increase in nodding to a female model compared to the absence of a female model in the ‘no model’ condition ($\chi^2_1 = 47.5$, p < 0.0005, one-tailed) was three times the increase in nodding seen when a female model was added to a male model to form a pair ($\chi^2 = 5.0$, p < 0.025 one-tailed, Table 3). The three-way interaction (male status × model male presence × model female presence) was not significant ($\chi^2 = 0.0$, NS, two-tailed).

It is tempting to conclude that single and paired males direct courtship signals more to single than to paired females. However, two factors complicate the interpretation of the male model/pair model comparison and make this conclusion unsafe. First, head nodding to a male model may diminish when it is accompanied by a female model if a paired male is seen as a lesser threat as a sexual competitor than an unpaired male. Second, signals to a pair may be simultaneously directed at both male and female. For both these reasons interpreting the difference in signalling to a male model and to a model pair as representing signalling that is directed only at a female may underestimate its true value. If this is the case, then males may not be directing courtship more to single than to paired females.

Single males are predicted to attempt courtship more than paired males attempt extra-pair courtship for several reasons. An extra-pair courting male might be abandoned by his mate; his attempts might be inhibited by his mate and thus less successful; a courted female may be less willing to copulate or pair with an already paired male; a paired male may be attempting EPC or repairing whereas a single male is probably attempting to pair, and the reproductive success of pairing is probably greater than that of an EPC; and single and paired males might differ in attractiveness (Reynolds, 1993). This prediction was supported for head nodding; single males nodded significantly more to the models of a pair, a female and a prone female than did paired males (weighted probabilities: 0.17 and 0.07, respectively; $\chi^2_1 = 100.1$, p < 0.0005, one-tailed). The model effect was significant for single males ($\chi^2_2 = 30.7$, p < 0.001, two-tailed), who nodded increasingly to pairs, females and prone females respectively, but not for paired males ($\chi^2_2 = 1.0$, NS, two-tailed, Table 3). The significant interaction between
The pattern of responses to the models cannot be explained as expressing some general (non-sexual) social function, such as gregariousness, since harlequin pairs are not gregarious in the breeding season and both proximity and display responses varied with the sexes of the model(s) in ways predicted by mate guarding and courtship hypotheses. Since harlequin tend to match the display of the opponent in an encounter (Inglis et al., 2000) the rarity of escalation to the most aggressive threat and attack stage against models is probably explained by the fact that model birds made no response to the head nods of real birds. This is, of course, a limitation of the use of stationary model animals. Nevertheless, the validity of inferring behavioural function from responses to the models is supported by the observations that during the experiments: (a) paired males did occasionally respond to models using the most aggressive ‘extended neck’ display as well as with the less aggressive head nod (Inglis et al., 1989, 2000); (b) single males always defended both prone female and single female models aggressively from other males; (c) single males often remained close to a prone female model for hours, pecking it on the back of the head (a precopulation behaviour; Inglis et al., 1989), and occasionally attempting to mount it; and (d) a paired female once attacked a prone female model.

We conclude that both members of a pair guard the mate from sexual competitors by spatial intervention and by signalling with the head nod. This extends our earlier conclusion concerning the existence of mate guarding by the male alone, inferred from observations of natural interactions (Inglis et al., 1989). The existence of female mate guarding was not apparent in these observations, but has been revealed by the model experiments (see also Mougeot et al., 2001). Although paired males did not head nod more
than single males to a male model, observations of real harlequin encounters (Inglis et al., 1989, 2000) indicate that head nodding is almost certainly a male mate guarding signal. Our results therefore suggest that head nodding also has a function in other male-male contexts, of equal value to paired and unpaired males; perhaps competition over resting sites, occupied by the models in these experiments.

Males mate guarded more intensely against single sex models than did females, as predicted, in terms of head nodding, but not in terms of relative proximity. Against model pairs too the prediction was unsupported for relative proximity, females in fact being closer than their mates to the model pair. This suggests that while both sexes seem to employ proximity as a mate guarding tactic they differ in the way they integrate it with other behavioural tactics as part of a strategy of mate retention that in total is predicted to claim more investment in males. Females responded adaptively to infidelity risk, mate guarding more intensively (measured both by proximity and head nodding) as the availability of an extra-pair female to their mate increased.

Single and paired males use the head nod to signal courtship as well as extra-pair courtship and/or EPC intention. Single males head nodded more to females than did paired males, for reasons already discussed, and single males nodded increasingly to more available females. In contrast, paired males head nodded equally to models of guarded and unguarded females and this may reflect either equal interest or greater inhibition in the presence of the unguarded female models as a result of the more intense female mate guarding that was shown against these models. The head nod is clearly a multifunctional signal, a phenomenon known in some other waterfowl (McKinney et al., 1990; McKinney, 1992). It is unlikely that females head nodded in the experiment to mate guard by soliciting copulation from the mate since only about 10% of copulations are preceded by female head nodding (Inglis et al., 1989).

Male mate guarding may function to prevent EPCs, to protect the female from predators and interference while feeding, or to prevent mate loss to another male (McKinney, 1985, 1988; Port, 1999). The last function would gain added benefit by the fact that harlequin pairs often reunite in successive seasons (Bengtson, 1972; Gowans et al., 1997; Robertson et al., 1998) and re-mating with the same partner may bring reproductive advantages (Rowley, 1983; Gowans et al., 1997). Consistent with this interpretation of mate guarding, male nodding to extra-pair females might signal courtship rather
than EPC attempts (Oring & Sayler, 1992), as in the canvasback *Aythya valisineria* (Anderson, 1984), functioning to test the interest of a new female in pairing (McKinney & Stolen, 1982). Since EPCs were rare or absent; we never observed a paired female leaving her mate for another male (Inglis *et al.*, 1989); and we never observed predation attempts, the precise function of both nodding to extra-pair females (courtship or EPC attempt) and mate guarding remains uncertain. In line with our prediction, females, far from seeking extra-pair copulations, are known to incite their mate to attack other males, in common with some other duck species. Females incite by extending the neck and head nodding to their mate, sometimes before nodding directly at the intruding male (Inglis *et al.*, 1989, 2000). Thus, the head nodding by females in the presence of model males probably reflects this natural context for the display. Female fidelity and mate guarding by both sexes seem to be successful in maintaining strict monogamy in the harlequin (Inglis *et al.*, 1989).

An apparent absence of EPCs and mate switching does not necessarily mean that males are not attempting these tactics. The experiments show, in fact, that they are attempting at least one of them, but are probably denied success by the close mate guarding practised by their mates. The experiments therefore point to an unsuspected dynamic of attempted, but failed, extra-pair reproductive attempts by males that was not revealed by detailed observational studies alone (Inglis *et al.*, 1989, 2000). This, and the discovery of previously unsuspected female mate guarding in this species, suggest a valuable role for model experiments in unravelling the complexities of sexual strategy. More theory on the coevolution of guarding and sexual strategy is needed to explain how one strategy, say extra-pair courtship, might be maintained in the population even though the coexistence of another, say close mate guarding, renders it futile (Petrie & Kempenaers, 1998). Such a seemingly paradoxical evolutionary scenario has been predicted for agonistic interactions (Maynard Smith & Parker, 1976), in which false signals of resource holding power can coexist in an evolutionary model with the ability to see through such deceptive signalling, thus rendering it ineffective.

**References**


