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Testing the behavioural dominance and dispersal hypothesis in Pochard

Sharmila Choudhury and Jeffrey M. Black

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Wintering flocks of diving ducks often show a great disparity in sex ratio with males predominating. The behavioural dominance and dispersal hypothesis explains this phenomenon by arguing that males dominate and exclude females from limited food sources, forcing them to migrate further south. Our study of a wild flock of Pochard *Aythya ferina* under manipulated feeding conditions, provides some support for this hypothesis. Male attacks were directed more at females (74%) than at other males (26%) even though the sex-ratio favoured males 4.7 to 1. Male dominance appeared to influence the timing of female foraging activity rather than foraging location. Females appeared to feed after the requirements of males were fulfilled. We suggest, that in the long run, feeding second may be energetically expensive to females and cause them to migrate further, where food supply may be more abundant and male competition less.

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In many species of diving duck, females migrate further south than males, producing a disparity in the sex ratio in wintering flocks (Alexander 1983, Owen and Dix 1986). The main hypotheses attempting to explain this phenomenon are: (1) Sexual dimorphism in body size may render females more susceptible to harsh weather, causing them to migrate further south (Ketterson and Nolan 1976, Saylor and Afton 1981). (2) Males may winter closer to the breeding grounds in order to return earlier in spring and acquire better breeding sites (Gauthreaux 1978, Myers 1981). (3) Females may require different food (e.g. insectivorous), only obtainable further south, to attain breeding condition (Ankney and Scott 1980). (4) There may be a higher female mortality due to greater energetic costs and predation pressures during incubation (Lack 1954, Ricklefs 1972). (5) Under limited food conditions in winter, male dominance may result in a reduced food intake of females and their exclusion from the best food sites, forcing

them to move to poorer foraging sites (Gauthreaux 1978). Segregation between males and females might be expected to occur both locally, with males occupying the better positions and females the peripheral areas (see Sutherland and Parker 1985), or over a wider geographical region with males wintering north and females having to migrate further south.

In this study we attempt to test this last behavioural dominance and dispersal hypothesis using observations from the European Pochard *Aythya ferina*. Of all diving ducks in Britain, this species has the greatest disparity in sex ratio in the wintering population with only 29.5% females (Owen and Dix 1986).

From Gauthreaux's hypothesis the following predictions were investigated: (1) males dominate females in aggressive encounters; (2) males monopolize good food sites, whereas females feed in sub-optimal areas; (3) females that remain in the better food sites have re-

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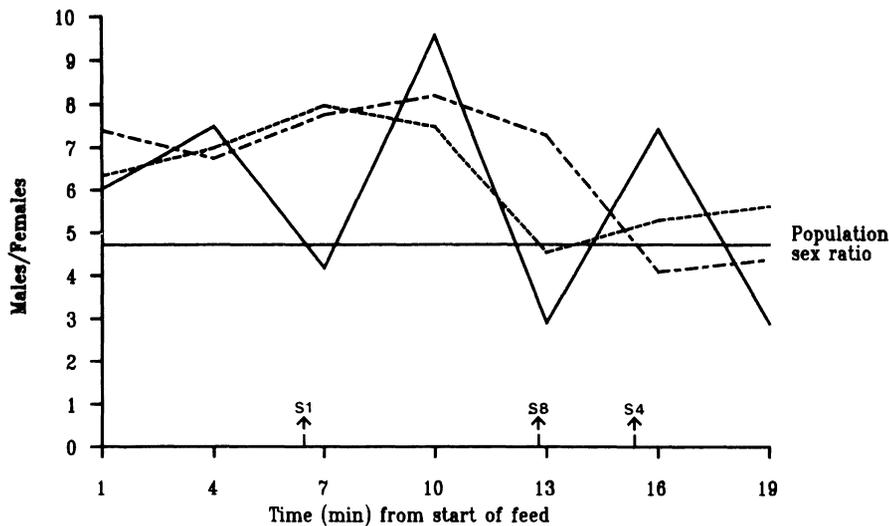


Fig. 1. Change in sex ratio during a feeding session when 1, 4, and 8 scoops of grain were scattered into the patch (1 scoop = 550 g). Standard errors ranged from 0.3–3.3, 0.6–2.0 and 0.8–2.6 for the three treatments. The arrows on the x-axis (S1, S4, S8) denote the time when the proportion of males dropped to match the mean population sex ratio. — = 1 Scoop, ---- = 4 scoops and = 8 scoops.

stricted access to the food and hence a poorer feeding success.

Methods

We studied wintering Pochard in the winter 1987/88 on a shallow lake of 1 ha at the Wildfowl & Wetlands Trust, Slimbridge, where grain is provided daily for birds. Other waterfowl frequent this lake, but Pochard were the predominant diving species. The site is located in the northern half of the species' winter range, where the sex ratio is greatly biased towards males. Food density was manipulated in a study patch of 5 m x 8 m water surface and 2 m depth.

Experiment 1. In order to investigate local habitat segregation by the two sexes we varied the quantity of food inside the study patch by scattering either 1, 4, or 8 scoops of wheat grain per feed (1 scoop = 550 g). Each scoop treatment was repeated 6–8 times in a random order. We attempted to disperse the grain (which sank to the bottom of the pond) uniformly throughout the patch. Some food was also distributed outside the patch to ensure that all birds received at least some food, but this was always at a density below the 1 scoop treatment in the study patch. The birds were fed three times a day: in the morning, at midday, and in the evening. Birds were allowed five minutes to settle down to feeding, after which sex ratios within the patch were determined every 3 min for 20 min. A pilot study had revealed that feeding sessions tended to last about 30 min, few birds remaining in the patch after this. We assume that the food both inside and outside the patch was totally consumed by the birds during each feeding session, since the density of birds was very high, with 800 Pochard present at the site. We thus also assume that patch

quality deteriorated with time, as birds depleted the food source. All intersexual aggressions were recorded during the feeding sessions.

Experiment 2. Feeding performance and aggressive encounters of both sexes were monitored by focal sampling. Six scoops of grain (3.3 kg) were thrown into the patch at feeding times, and attempts were made to alternate sampling of males and females during the 30 min feeding sessions. When an individually identifiable bird (with colour-dyed feathers or some other distinguishable plumage characteristic) entered the patch, it was observed for as long as it stayed within it. We recorded the dive rates (number of dives per unit time), the dive lengths (time under water) and all aggressive encounters during the feeding sessions.

Results

The mean sex ratio of the 800 Pochard wintering at the site during the observation period was 4.7 males per female (SE = 0.15). Despite this predominance of males in the flock, most male aggression was directed towards females. Of 70 aggressive attacks by males, significantly more (74%) were directed at females than at other males (26%) ($\chi^2 = 151.95$, $p < 0.001$); the population sex ratio was used to calculate expected values for aggressive attacks by sex, since the sex ratio in the patch never varied significantly from the population sex ratio (see below). Males also initiated significantly more attacks than females ($\chi^2 = 19.02$, $p < 0.001$). For both sexes, birds which initiated attacks won them on 99.6% of occasions ($N_M = 234$, $N_F = 23$).

Under all three treatments (1, 4 or 8 scoops of grain) the total number of birds within the patch decreased from the beginning to the end of a feeding session. The

mean number of birds under each treatment after 1, 10 and 19 min, respectively, was: 1 scoop = 29, 22, 15 (N = 6); 4 scoops = 74, 30, 16 (N = 8); 8 scoops = 70, 32, 16 (N = 8). An ANCOVA comparing sex ratios between grain densities with time as covariate indicates that the proportion of males within the patch was significantly higher at the beginning of feeding sessions, when the grain density was highest, and decreased as food supply was depleted ($F = 6.117$, $df = 1$, $p = 0.015$, $N = 141$). The trend in sex ratio with respect to time was the same for all three treatments ($F = 0.092$, $df = 2$, $p = 0.912$). However, there was no significant difference in sex ratio between the three treatments ($F = 0.533$, $df = 2$, $p = 0.588$, $N = 141$), i.e. larger amounts of food put out did not result in a higher proportion of males entering the patch.

The rate of change in the proportion of males during the feeding session was substantially slower at the higher grain densities. It took an average of 12.5 min after 8 scoops or 15 min after 4 scoops for the observed sex ratio in the patch to drop to the level of the mean population sex ratio, whereas after the 1 scoop treatment this level was matched in 6 min (Fig. 1).

We attempted to quantify food intake of both sexes by measuring dive times and diving rates. Since the proportion of males was higher at the beginning of feeding sessions than at the end, we divided the diving data in two (collected in first 10 min or last 20 min) so as to obtain roughly similar number of samples in each category.

The mean dive rate of both sexes was higher (2.6 min^{-1} , $SD = 0.5$, $N = 67$) in the first 10 min than in the last 20 min (2.3 min^{-1} , $SD = 0.6$, $N = 48$) of the feeding session ($t = 2.915$, $p = 0.004$). The mean dive length was significantly shorter at the beginning (16.9 s , $SD = 3.8$, $N = 102$) compared with the end (18.4 s , $SD = 3.9$, $N = 69$) of feeding sessions ($t = 2.438$, $p = 0.016$). However, there was no difference between the sexes in either dive rates (beginning, $t = 0.423$, $p > 0.6$, $N = 68$; end, $t = 0.133$, $p > 0.8$, $N = 48$) or dive lengths (beginning, $t = 0.701$, $p > 0.4$, $N = 102$; end, $t = 0.03$, $p > 0.9$, $N = 69$) during the beginning (first 10 min) and end (last 20 min) of a feeding session.

Discussion

Several studies provide only partial support for the behavioural dominance theory by demonstrating male dominance over females (Alexander and Hair 1979, Hepp and Hair 1984), without showing a reduction in feeding performance of females or their exclusion from preferred food sites. However, dominance relationships can only have ecological significance if they adversely affect some fitness component of the subordinate (Greenberg 1986).

Our results are consistent with the first prediction

that males dominate females in aggressive encounters. There also seems to be evidence for the second prediction that males exclude females from food sites on a local scale. However, we were unable to prove our third prediction, that male dominance results in a reduction in the feeding efficiency of females.

Exclusion from a food source can take place in two ways: (1) Spatial exclusion – when subordinates have restricted access to a feeding site, being permitted to feed only in the suboptimal areas (Goss-Custard et al. 1984). (2) Time exclusion – when subordinates are only allowed to feed after dominants have had their fill and left the patch (Barnard 1984).

Dominance relationships may result in one or both means of exclusion simultaneously. We suggest that in our study, the male bias at the beginning of feeding sessions, when food was plentiful, was due to female exclusion from the site. As the food supply was depleted and males left the patch, presumably satiated, the proportion of females increased. A similar effect of delayed timing of feeding activity of subordinates has been shown in jays (Craig et al. 1982) and swans (Black and Rees 1984).

To our knowledge two studies on diving ducks in North America have provided evidence for spatial segregation of the sexes on a local scale due to feeding competition. Nichols and Haramis (1980) found that in Canvasbacks *Aythya valisineria* higher proportions of males occurred in large open bodies of water, whilst females tended to frequent smaller outlying waters, and that females generally occupied peripheral areas of flocks. Alexander (1987) determined that a greater proportion of male Canvasbacks consistently utilised the best of two impoundments, as determined by duck counts and biomass assessments of the tubers on the bottom of the ponds.

We were unable to show differential distributions of the two sexes in different quality food patches. Although females were always temporarily excluded from the study patch at the beginning of feeding sessions, the quantity of food put out had no effect on the proportion of females approaching it. This might be explained if poached are unable to sample the food quantities in a patch accurately. However, since the total number of birds in the patch increased with quantity of food put out, this is unlikely to be the case.

It seems more likely that females have adopted a strategy of feeding later in order to avoid aggressive encounters with males. It is possible that this feeding pattern reflects differing foraging strategies of males and females. Different foraging strategies for the sexes or for the same sex under different conditions have been demonstrated in a number of species (Wallace 1974, Draulans 1982). Females may have lower energetic requirements than males because of their smaller body size and may still be able to obtain sufficient food by waiting until most of the males have left the food patch. A subordinate strategy of feeding second and thus

avoiding aggressive interactions with males may in this case be a sound ESS.

However, in patches with unrenewable food sources, as in our site, patch quality deteriorates with time spent foraging in it. Since intake rate is known to be higher in better food patches (Parker and Sutherland 1986), it seems likely that females suffer a reduced intake rate by feeding after the quality of the food patch has deteriorated. Prop and Loonen (1988) quantified, in terms of an individual's intake, the importance of being first in a food patch. They found that the first 8 geese (in a flock of 67) to enter a patch of vegetation removed 50% of the available leaves and by the 59th goose all the leaves had been removed, leaving none for the last 8 birds.

A strategy of feeding second can only be successful if the costs of aggressive encounters with males are greater than the costs of feeding later. We attempted to measure the costs of aggressive encounters to females in terms of food intake. We assumed that food intake was directly related to dive rate and dive length and found no difference between the sexes. However, we have no knowledge of the actual food intake of each bird, and there may have been inhibition of female feeding by male supplanting under water. Underwater aggressive encounters have been witnessed in Canvasbacks in a tank with glass sides (J. Ball unpubl. data). In addition, it is possible that males and females differ in foraging efficiency, for instance that males obtain more food per mouthful (see Draulans 1982, Koehl et al. 1984) due to their larger body size.

Alternatively, there may be costs other than just food intake involved, which persuade females to avoid encounters with males. More detailed studies of individually marked birds are needed to investigate various female traits and fitness components in relation to intersexual competition.

Finally, it is possible that the costs of feeding later may be very small. This will be the case if food is not limiting as we had assumed, so that females are still able to obtain sufficient food after males have fed in the patch. We believe that the food we provided at each feed was insufficient to fulfil the requirements of 800 birds and that food should thus have been limiting. However, since Pochard feed mainly at night and on a variety of plant and animal foods (Cramp et al. 1977), it is possible that the daytime feeds of wheat grain only provided a supplement to their diet. The majority of the ducks in fact left this site (where there is no natural aquatic vegetation) each night (pers. obs.), presumably to feed in surrounding habitats.

Although our study situation was somewhat artificial, since Pochard usually feed in less dense flocks on less concentrated food sources, and a lot of their feeding activity occurs at night, we believe that the results of our study can be related to less dense feeding situations. We have shown that females appear to feed after the requirements of males are fulfilled, irrespective of the quantity of food available. We would thus expect to see

females excluded temporarily from any food patch discovered by a flock of Pochard. In the long run, feeding second may be energetically expensive to females in the wild. We suggest that this could be why females migrate to more southerly latitudes, where food supply may be more abundant and male competition less.

In conclusion, we suggest that female Pochard wintering in northern latitudes do suffer some energetic costs by remaining in the same habitat as males, but that further investigations are required to reveal the exact nature of the costs involved. We recommend that future tests of the dominance and dispersal hypothesis should attempt to measure actual food intake of each sex and other potential fitness components of females that could be negatively affected by male dominance. Whether or not these behavioural differences on a local scale reflect distribution patterns on a large scale has yet to be tested (see Rogers et al. 1989).

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References

- Alexander, W.C. 1983. Differential sex distributions of diving ducks (Aythyini) in North America. – *Amer. Birds* 37: 26–29.
- 1987. Aggressive behavior of wintering diving ducks (Aythyini). – *Wilson Bull.* 99: 38–49.
- and Hair, J.D. 1979. Winter foraging behavior and aggression of diving ducks in South Carolina. – *Proc. Ann. Conf. S.E. Assoc. Fish and Wildl. Agencies* 31: 226–232.
- Ankney, C.D. and Scott, D.M. 1980. Changes in nutrient reserves and diet of breeding brown-headed cowbirds. – *Auk* 97: 684–696.
- Barnard, C.J. 1984. The evolution of food scrounging strategies within and between species. – In: Barnard, C.J. (ed.) *Producers and scroungers*. Croom Helm, Australia, pp. 95–126.
- Black, J.M. and Rees, E.C. 1984. The structure and behaviour of the whooper swan population wintering at Caerlaverock, Dumfries and Galloway, Scotland. – *Wildfowl* 35: 21–36.
- Craig, J.L., Stewart, A.M. and Brown, J.L. 1982. Subordinates must wait. – *Z. Tierpsychol.* 60: 275–280.
- Cramp, S. and Simmons, K.E.L. (eds.) 1977. *The birds of the western Palearctic*. Vol. I. Oxford University Press, Oxford.
- Draulans, D. 1982. Foraging and size selection of mussels by the tufted duck (*Aythya fuligula*). – *J. Anim. Ecol.* 51: 943–956.
- Gauthreaux, S.A. 1978. The ecological significance of behavioural dominance. – In: Bateson, P.P.G. and Klopfer, P.H. (eds.) *Perspectives in ethology*. Vol. 3. Plenum Press, New York, pp. 17–54.
- Goss-Custard, J.D., Clarke, R.T. and Durell, S.E.A. le. v. dit. 1984. Rates of food intake and aggression of oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe Estuary. – *J. Anim. Ecol.* 53:233–245.

- Greenberg, R. 1986. Competition in migrant birds in the non-breeding season. – In: R.F. Johnston (ed.). Current ornithology. Vol.3. Plenum Press, New York, pp.281–307.
- Hepp, G.R. and Hair, J.D. 1984. Dominance in wintering waterfowl (Anatini): effects on distribution of sexes. – *Condor* 86: 251–257.
- Ketterson, E.D. and Nolan, V. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis hyemalis*). – *Ecology* 57: 679–693.
- Koehl, P.S., Rothe, T.C. and Derksen, D.V. 1984. Winter food habits of Barrow's goldeneyes in southeast Alaska. – In: D.N. Nettleship, Sanger, G.A. and Springer, P.F. (eds). Marine birds: their feeding ecology and commercial fisheries relationships. Canadian Wildlife Service, Dartmouth, pp. 1–5.
- Lack, D. 1954. The natural regulation of animal numbers. – Clarendon Press, Oxford.
- Lovvorn, J.R. 1989. Food defendability and antipredator tactics: implications for dominance and pairing in canvasbacks. – *Condor* 91: 826–836.
- Nichols, J.D. and Haramis, G.M. 1980. Sex-specific differences in winter distribution patterns of canvasbacks. – *Condor* 82: 406–416.
- Owen, M. and Dix, M. 1986. Sex ratios in some common British wintering ducks. – *Wildfowl* 37, 104–112.
- Parker, G.A. and Sutherland, W.J. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. – *Anim. Behav.* 34: 1222–1242.
- Prop, J. and Loonen, M. 1988. Goose flocks and food exploitation: the importance of being first. – In: Quellet H. (ed.). Acta XIX Congr. Int. Ornithol. Vol. II. University of Ottawa Press, Ottawa, pp. 1878–1887.
- Ricklefs, R.E. 1972. Fecundity, mortality and avian demography. – In: D.S. Farner (ed.). Breeding biology of birds. National Academy of Sciences, Washington D.C. pp.366–447.
- Rogers, C.M., Theimer, T.L., Nolan, Jr.V. and Ketterson, E.D. 1989. Does dominance determine how far dark-eyed juncos *Junco hyemalis* migrate into their winter range? – *Anim. Behav.* 37: 498–506.
- Sayler, R.D. and Afton, A.D. 1981. Ecological aspects of Common Goldeneyes *Bucephala clangula* wintering on the upper Mississippi River. – *Ornis. Scand.* 12: 99–108.
- Sutherland, W.J. and Parker, G.A. 1985. Distribution of unequal competitors. – In: R.M. Sibly and R.H. Smith (eds). Behavioural ecology: consequences of adaptive behaviour. Blackwell Scientific Publications, Oxford, pp.255–273.
- Wallace, R.A. 1974. Ecological and social implications of sexual dimorphism in five melanerpine Woodpeckers. – *Condor* 76: 238–248.