CHANGES IN THE FREQUENCY OF PROSPECTING FLY-OVERS 
BY MARSH HARRIERS *CIRCUS AERUGINOSUS* IN RELATION TO 
SHORT-TERM FLUCTUATIONS IN DABBLING DUCK ABUNDANCE 

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Fritz H., M. Guillemaïn & S. Guérin 2000. Changes in the frequency of 
prospecting fly-overs by Marsh Harriers *Circus aeruginosus* in relation to 

Wintering waterfowl gathering in large flocks during the day may be attractive 
to avian predators in a way similar to that of bird colonies. The response 
of Marsh Harriers to changes in dabbling duck abundance was monitored 
on four freshwater sites in the marshes of western France, a major wintering 
region for wildfowl in the country. The number of harriers present at each 
site remained stable throughout the winter. However, the frequency of pros- 
specting fly-overs by harriers, i.e. search effort, increased with duck abun- 
dance. Frequency of fly-overs was also affected by the number of conspe- 
cifics present on the site, wind velocity and time of the day, and varied 
between months. All these factors are discussed in relation to prey avail- 
ability, competition, and minimization of energy expenses while searching. 
‘Female morph’ harriers appeared to scout more over duck flocks than 
‘male morph’ harriers, which is consistent with the fact that sexual segrega- 
tion in feeding habits is often recorded in dimorphic raptors. Direct preda- 
tion was rarely seen but ducks always reacted to the fly-overs of harriers. 
The raptors were responsible for up to 130 disturb- 
ances per day and the 
number of disturb- 
ances was correlated to the number of ducks present. The 
activity of harriers may therefore affect the behaviour of dabbling ducks, 
hence the quality of their wintering quarters.

Key words: *Circus aeruginosus* - dabbling ducks - disturbance - Marsh 
Harrier - predator-prey interaction - prospecting fly-overs

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INTRODUCTION

Responses of predators to changes in prey abundance may be numerical or functional (Holling 1959). Both responses have been described for raptor species in relation to fluctuations in small rodents populations (Korpimäki & Nor- daahl 1991a). The short-term numerical response of avian predators depends largely on their mobility (Korpimäki 1985). The functional response is more closely linked to the relative availability of the main and alternative prey, the ability to adjust search effort and to shift from one category of 
prey to another (Andersson & Erlinge 1977). Consequently, nomadic specialists tend to exhibit strong numerical responses whereas resident generalists mostly show functional responses (Phelan & Robertson 1978; Korpimäki & Nor- daahl 1991b).

Attractiveness to their predators is often cited as a potential cost of bird colonies, mostly through numerical responses although functional responses can occur (Winttenberger & Hunt 1985). Wintering waterfowl gathering in large flocks during the day should also attract avian predators in a similar way. Bald Eagles *Haliae-
*tus leucocephalus* seem to commonly associate with winter concentrations of waterfowl (Baldassare & Bolen 1994). Large flocks of wintering dabbling ducks, particularly Teal *Anas crecca* in the Camargue, also appear attractive to large raptors (Tamisier 1974). However, very little is known about the relationship between wintering duck abundance and avian predators response (Owen & Black 1990), probably because predators represent a minor cause of death for wildfowl (Stout & Cornwell 1976).

The Marsh Harrier *Circus aeruginosus* is a generalist predator that prefers hunting over tall vegetation, mainly at the edge of fresh or brackish water ponds, principally using surprise as a hunting technique (Schipper *et al.* 1975; Cramp & Simmons 1980; Clarke *et al.* 1993). Marsh Harriers are known to attack ducks during the winter, but primarily feed on weak individuals, wounded or sick, or even scavenge (Tamisier 1970; Schipper 1973; Clarke *et al.* 1993). In the marshes of western France, a major wintering region for wildfowl in the country (Ridgill & Fox 1990), Marsh Harriers were found to feed mainly on mammals, with wildfowl being only an alternative prey (Bavoux *et al.* 1990). However, during the winter 1995-96, the first year of a general survey of factors affecting the distribution and structure of the dabbling duck community in the marshes of western France, we found that Marsh Harriers were very active over large flocks of ducks, and seemed to be a major source of disturbance for the wintering dabbling duck population. Hence, we decided to monitor the response of Marsh Harriers to changes in dabbling ducks abundance on four freshwater sites in the marshes of western France, and evaluate the intensity of disturbance caused by the raptors.

**METHODS**

Data were collected from October 1996 to February 1997 on four open water-bodies, from 6.5 to 32 ha, in the region of Rochefort, western France (45°60'N, 01°00'W). These sites belong to four nature reserves, three of them managed by the ‘Ligue française pour la Protection des Oiseaux’ and the last one by the ‘Fédération Départementale des Chasseurs de Charente-Maritime’. Each site was visited once a week, and observations were carried out from dawn to dusk with a 20x telescope and 10x binoculars. The day was divided into four observation periods, hereafter referred to as time class variable: from 07:00-10:00h, 10:00-13:00h, 13:00-16:00h and 16:00-19:00h in October and February, and from 08:00-10:30, 10:30-13:00, 13:00-15:30 and 15:30-18:00 from November to January. Three weather variables were noted, CLOUD (from 0 = sunny to 3 = completely overcast), RAIN (from 0 = no rain to 3 = heavy rain), and WIND (from 0 = no wind to 3 = strong wind). Duck counts were made twice in each observation period. Counts of harriers simultaneously present around the site were made once in each observation period. Fly-overs by harriers and other raptor species were monitored as continuously as possible throughout the observation period. We concentrated our study on the Marsh Harriers since they constituted 90% of all potential avian predators for ducks on the sites, Buzzards *Buteo buteo* were resident at two sites, Hen Harriers *Circus cyaneus*, Peregrine Falcon *Falco peregrinus* and Herring Gull *Larus argentatus* were occasional visitors. A prospecting fly-over was defined as a bird flying low (< 20 m) over the ducks and inducing reactions from the ducks. This behaviour was defined as prey searching by Tamisier (1970) since it may allow the harrier to isolate a sick or wounded duck.

As previously pointed out in other studies, it was not always possible to distinguish between adult female, juvenile female and juvenile male (Schipper *et al.* 1975). This is particularly true in western France were even adult males are very polymorphic (Bavoux *et al.* 1988, 1993). Hence, we classified the birds into two groups: the male morph - all individuals with large patches of grey on the wings -, and the female morph - all the other individuals - (Schipper *et al.* 1975). We did not classify those individuals when poor visibility did not allow the detection of grey patches. We
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recorded every activity while one individual harrier scouted the water, but most of the outcome of the hunting actions could not be seen due to dense vegetation. We examined changes in the frequency of prospecting fly-overs with variations in duck abundance. This is a similar approach to that of Szép & Barta (1992), who quantified the response of Hobbies *Falco subbuteo* to changes in colony size of Bank Swallows *Riparia riparia* through changes in attack rate. We divided the total number of fly-overs by the number of harriers counted at the site in order to take into account the differences in raptor population between sites; this gave an estimate of an average individual frequency of passes (i.e. search effort) for each site. At each site, the observations were made from exactly the same place. Duck abundance and the frequency of passes by harriers had a Poisson-type distribution and were square-root transformed in order to meet the normality constraint of parametric statistical analyses (Sokal & Rohlf 1995). Disturbance intensity, i.e. the sum of fly-overs per minute, was not transformed since we only used it in non-parametric statistical analyses.

RESULTS

Marsh Harrier response

We did not find any variation in harrier numbers within sites. In the 'Station de Lagunage' (Lagunage) and the 'Réserve des Marais d'Yves' (Yves), the maximum number of Marsh Harriers counted around the water were always the same, respectively 3 and 4. For the two other sites, the 'Réserve de Breuil-Magné' (Breuil) and the 'Réserve de Moëze' (Moëze) the number of harriers was respectively 8 and 12. The maximum numbers of harriers present on the sites were not significantly correlated with the number of ducks (Spearman rank: $r_s = 0.8, n = 4$, n.s.; Fig. 1). We then classified the sites in two groups: PRED1 with number of harriers < 7 and PRED2 with number of harriers > 7. There were significant differences between sites for both duck abundance and the individual frequency of fly-overs by harriers ($F_{3,221} = 250.26, P < 0.001$ and $F_{3,221} = 8.65, P < 0.001$, respectively; Fig. 1).

The results of the covariance analysis between the individual frequency of fly-overs and the abundance of ducks with SITE, MONTH, TIME, WIND, CLOUD, RAIN and PRED as factors showed that the relationship between frequency of fly-overs by harriers and duck abundance was significant and positive. TIME, MONTH, WIND and PRED were also significant in the model (Table 1). None of the interactions were signifi-

Table 1. Results of the Analysis of Covariance on the individual frequency of passes by harriers with the abundance of ducks as a covariate (square-root transformed), and PRED, MONTH, TIME and WIND as class variables. ($n = 225, Model R^2 = 0.31$).

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of Square</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>duck abundance</td>
<td>0.087</td>
<td>1</td>
<td>34.51</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>PRED</td>
<td>0.039</td>
<td>1</td>
<td>5.38</td>
<td>0.021</td>
</tr>
<tr>
<td>MONTH</td>
<td>0.039</td>
<td>4</td>
<td>5.70</td>
<td>0.001</td>
</tr>
<tr>
<td>TIME</td>
<td>0.043</td>
<td>3</td>
<td>3.51</td>
<td>0.016</td>
</tr>
<tr>
<td>WIND</td>
<td>0.026</td>
<td>4</td>
<td>3.85</td>
<td>0.005</td>
</tr>
</tbody>
</table>

Fig. 1. Number of Marsh Harriers counted, average frequency of prospecting fly-overs by Marsh Harriers per individual (fly-overs min$^{-1}$, and SE bars) and duck abundance for each site of the study (both frequency and abundance are square-root transformed).
The frequency of fly-overs was higher for sites with low number of harriers (Fig. 2). The frequency of fly-overs increased with wind velocity, decreased with time of the day and varied between months (Fig. 3). All these factors combined may explain the difference between sites since SITE was not significant anymore once all these variables had been inputted into the model.

We compared whether the proportion of passes made by 'Female morph' and by 'Male morph' harriers reflected the proportion of individuals counted on the site, and we found that 'Female morphs' did more scouting over the water-bodies than did the 'Male morphs' (Table 2).

**Disturbance intensity**

Only nine complete pursuits (3 female and 2 male Mallard *Anas platyrynchos*, 2 female and 1 male Teal, 1 female Wigeon *Anas penelope*) were recorded; none was successful. Harriers were seen feeding on ducks on six occasions: 2 Mallards (one male and one female), 2 Teals and 2 Wigeons (not sexed).

The increase in the frequency of fly-overs by harriers with the number of ducks meant an increase in the level of disturbance for large flocks. In addition, the average disturbance intensity (number of fly-overs min⁻¹) over the winter per site was correlated with the number of harriers on the site (Spearman rank: $r_s = 1.0, n = 4, P = 0.05$).

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**Fig. 2.** Relationship between the average frequency of prospecting fly-overs by Marsh Harriers per individual (fly-overs min⁻¹, and SE bars) and the abundance of ducks, for sites with large number of harriers (black dots and full line) and sites with low number of harriers (white dots and broken line), (both frequency and abundance are square-root transformed). Equations are respectively: $y = 0.0018x + 0.0516$ and $y = 0.0013x + 0.0834$.

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**Fig. 3.** Variation in the average frequency per individual of prospecting fly-overs by harriers (fly-overs min⁻¹) with different classes of wind velocity, between the four observation periods, and between months.
Table 2. Results of the comparison of the proportion of the passes made by 'Male morph' and 'Female morph' harriers, with the proportion of 'Male morph' and 'Female morph' found in the population of harriers counted in each site. We tested whether the proportion of passes made by female and male morphs differed from the proportion of female and male morphs counted on the site.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Passes</th>
<th>Birds counted</th>
<th>$\chi^2$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Female morph</td>
<td>Male morph</td>
<td>Female morph</td>
<td>Male morph</td>
</tr>
<tr>
<td>Lagunage</td>
<td>102</td>
<td>24</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Moëze</td>
<td>561</td>
<td>35</td>
<td>10</td>
<td>2</td>
</tr>
<tr>
<td>Breuil</td>
<td>120</td>
<td>22</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Yves</td>
<td>111</td>
<td>38</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

Table 3. Average disturbance intensity (total number of passes min$^{-1}$) per month for each site. The number of disturbances day$^{-1}$ were calculated multiplying the value min$^{-1}$ by the number of daylight hours day$^{-1}$ month$^{-1}$ (9 for December, 10 for January and November, 11 for October and February).

<table>
<thead>
<tr>
<th>Month</th>
<th>Lagunage</th>
<th>Moëze</th>
<th>Breuil</th>
<th>Yves</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>min$^{-1}$</td>
<td>day$^{-1}$</td>
<td>min$^{-1}$</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>October</td>
<td>0.09</td>
<td>59</td>
<td>0.21</td>
<td>139</td>
</tr>
<tr>
<td>November</td>
<td>0.04</td>
<td>24</td>
<td>0.22</td>
<td>132</td>
</tr>
<tr>
<td>December</td>
<td>0.01</td>
<td>5</td>
<td>0.18</td>
<td>97</td>
</tr>
<tr>
<td>January</td>
<td>0.05</td>
<td>30</td>
<td>0.10</td>
<td>60</td>
</tr>
<tr>
<td>February</td>
<td>0.03</td>
<td>20</td>
<td>0.08</td>
<td>53</td>
</tr>
</tbody>
</table>

Monthly values of disturbance and duck abundance were correlated for three of the reserves: Moëze (Spearman rank: $r_s = 0.9$, $n = 5$, $P = 0.05$), Breuil (Spearman rank: $r_s = 0.9$, $n = 5$, $P = 0.05$) and Yves (Spearman rank: $r_s = 1.0$, $n = 5$, $P = 0.01$), whereas no relation was found for the Lagunage (Spearman rank: $r_s = 0.2$, $n = 5$, n.s.). The average number of disturbances varied from 0.01 min$^{-1}$ for the Lagunage in December to 0.22 min$^{-1}$ for Moëze in November (Table 3). Ducks reacted in three ways to harriers: by vigilance while staying still, grouping, or flying away. Out of a hundred fly-overs for which we qualified the reactions, on 44 occasions the group of ducks just stayed still, on 33 they swam and grouped, and on 23 they flew away.

DISCUSSION

Marsh Harriers showed no numerical response to changes in dabbling duck abundance. This result is consistent with the fact that Marsh Harriers are resident generalists in the marshes of western France, which means that they are more likely to respond functionally than numerically (Phelan & Robertson 1978; Korpimäki & Norðaahl 1991ab). Australasian Harriers *Circus approximans*, with similar characteristics, showed both responses in relation to changes in abundance of their primary prey (Pierce & Maloney 1989), a result often found for other raptor species (Phelan & Robertson 1978). Our study showed that Marsh Harriers modify their searching activity around water-bodies with changes in dabbling ducks abundance on these water-bodies.
The population of harriers hunting at each of our study sites during the winter period is likely to be driven by the abundance of mammals (Bavoux et al. 1990). One species, the Coypu *Myocastor coypus*, is subject to extensive culling operations in some areas in the marshes. This may play an important role in maintaining large groups of Marsh Harriers in winter through the availability of a large amount of carrion to feed on. This is the case in Breuil and Moëze, the two sites with the largest number of harriers counted.

Marsh Harriers at our study sites increased their search efforts with increasing number of dabbling ducks. This is consistent with the fact that the number of sick and wounded individuals is likely to increase with increasing duck numbers. The y-intercept of the relationship between the individual frequency of passes and the abundance of ducks was higher at sites with low numbers of harriers. This suggests that individual search effort is higher, for a given number of ducks, in sites with few conspecifics. This could mean that the intraspecific competition for ducks was too high at sites with large number of harriers (PRED2), and that search effort was not as beneficial as at sites with fewer harriers (PRED1). However, it is more likely that the reason for such a difference lies in the relatively greater availability of mammals, particularly Coypu, at sites with large number of harriers. An additional reason that might reduce the search effort in PRED2 site is the fact that once a carrion is found or a duck killed by one bird it may be easier for the others to locate it through a process similar to that of 'public information' (Krebs & Davies 1987); on three occasions we saw more than two individuals feeding successively from the same dead duck, one bird often chasing the other off. The frequency of passes in PRED1 sites showed a greater variability in response to changes in duck abundance than PRED2 sites, this was mainly due to variation in the Lagunage, where the proximity of the river Charente occasionally caused great disturbances when large boats passed close to our observation site.

The search effort of harriers was influenced by the abundance of ducks, however it also varied between months, and was particularly high in October. October is a month during which migrant Marsh Harriers often stop over in our study sites; this might have increased the actual number of birds patrolling the area. In January and February, large-scale poisoning operations are carried out as part of the Coypu eradication program. The lower frequencies of fly-overs observed in February could be explained by an increase in the availability of Coypu carrion. The time of day also influenced search effort by harriers, with decreasing effort towards dusk, which is consistent with the fact that an increased proportion of harriers may have found prey and be satiated as the day goes on. Moderate and strong wind favoured scouting activity by harriers. Birds, and raptors in particular, are known to use wind velocity to reduce energy expenses during flight (Rijnsdorp et al. 1981). Strong winds seem to increase flight manoeuvrability in harriers (Schipper et al. 1975), and allow them to maintain a very low flight speed by flying against wind (Elkins 1988), a situation very favorable to search for prey hidden in tall vegetation. The fact that rain seemed to have no influence on the frequency of fly-overs is surprising in the light of other raptor studies (Rijnsdorp et al. 1981). However, we had only 17 observation periods during rainy days, and this small sample size may explain why we do not detect any significant difference.

Female morphs seemed to scout more the water-bodies and water edges than did male morphs, which is consistent with the fact that females are bigger than males and less manoeuvrable, probably leading to an increased tendency to scavenge but also potentially inducing a specialisation on larger prey. Similar differences were found in Flevoland and in the Camargue where male Marsh Harriers hunted more often over short vegetation and cultivated fields, taking more agile prey than females (Schipper et al. 1975). Such sexual segregation in habitat choice and diet is often witnessed in highly dimorphic raptor species (see Newton 1979 for review).

The effects of disturbance by Marsh Harriers
on dabbling duck flocks appeared more important than direct effects through predation, as previously noted in the Camargue (Tamisier 1970). Our figures are similar to those found in the Camargue for Marsh Harriers, except for Moëze where disturbance is twice as frequent. The pattern of disturbance caused by the harriers was slightly different between months, with October values being very high and February comparatively low. Our results do not support the idea of a decrease in the number of daily disturbances with the increase in day length, but the intensity of disturbance was greater during the first half of the winter than in the second part, as found in the Camargue (Tamisier 1970). High levels of disturbance caused by raptors can severely reduce foraging efficiency of waterbirds (Quinn 1997), and waterfowl are known to be very sensitive to disturbance (Fox & Madsen 1997). Therefore Marsh Harriers may have more impact on wintering waterfowl populations through indirect effects than through direct predation: their activity may influence the time-budget of dabbling ducks, e.g. reduction in feeding time or increased energy expenses through flying, hence ultimately the quality of their wintering quarters (Hill et al. 1997).

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REFERENCES


SAMENVATTING

Grote troepen overwinterende watervogels kunnen, net als broedvogelkolonies, roofvogels aantrekken. In deze studie volgden wij gedurende één winter de reactie van Bruine Kiekendieven op veranderingen in de aantallen grondeleenden in vier meren variërend in grootte van 6,5 tot 32 ha. Deze meren liggen in de moerasachtige gebieden in het westen van Frankrijk, in de buurt van Rochefort, en zijn van groot belang voor overwinterende watervogels. Bij alle meren bleef het aantal kiekendieven opmerkelijk constant gedurende de winter. Het aantal door de kiekendieven uitgevoerde zoekvluchten nam echter wel toe met toenemende aantallen eenden. Ook was de zoekinspanning afhankelijk van het aantal soortgenoten, de wind, de tijd van de dag en de maand. Vrouwtjes (of eigenlijk vogels met een vrouwachtig voorkomen, want het geslacht is niet met zekerheid vast te stellen in deze tijd van het jaar) bleken vaker dan mannetjes de troepen eenden te inspecteren. Dit bevestigt de waarneming dat de manier van voedsel zoeken bij dimorfe roofvogels sterk geslachtsgebonden is. Slechts zelden werd gezien dat een eend daadwerkelijk geslagen werd. Wel reageerden de eenden altijd op de zoekvluchten van de kiekendieven. De roofvogels konden wel tot 130 keer per dag de eenden verstoren, en het aantal verstoringen was gecorreleerd met het aantal eenden. De activiteit van de kiekendieven beïnvloedt dus het gedrag van de eenden en daardoor ook de geschiktheid van een overwinteringgebied. (JvdM)

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