SHORT REPORT

Marsh Harriers *Circus aeruginosus* target Teals *Anas crecca* at roosts according to potential availability of vulnerable prey

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Capsule The mean daily rate of foraging flyovers by Marsh Harriers in a given site is better predicted by the number of vulnerable Teal they can force to take flight (equivalent to patch size) than by the total number of Teal present.

Functional and numerical responses, the increase in predator activity and numbers with increasing density of potential prey (Holling 1959) have been described and analysed for several raptor species (Andersson & Erlinge 1977, Phelan & Robertson 1978, Korpimäki & Nordaahl 1991, Redpath & Thirgood 1999). Waterfowl, especially dabbling ducks (Anatidae), commonly gather in great numbers on large waterbodies during daylight hours, and the attractiveness of such flocks to raptors has been documented (Tamisier 1974).

In a recent study, Fritz *et al.* (2000) showed that 31% of variance in the frequency of prospecting flyovers by Marsh Harriers *Circus aeruginosus* in wetlands could be explained by a model driven by the number of ducks present at these waterbodies. This was because Marsh Harriers often 'test' ducks by forcing them to take flight, and then attack the wounded or sick flightless individuals (Schipper 1973, Schipper *et al.* 1975, Clarke *et al.* 1993). The probability of a raptor finding a flightless duck is therefore likely to increase with the total number of ducks present. However, Marsh Harriers also rely on surprise as a hunting technique (Schipper *et al.* 1975, Clarke *et al.* 1993), and attempt to put ducks on the wing by flying over them. The ducks that do not see the raptor coming from a distance will take flight or be attacked, while those that see the harrier will swim away and not be pursued.

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If Harriers try to maximize their food intake rate (i.e. probability of success per flyover), we hypothesized that the frequency of prospecting flyovers by Marsh Harriers should be better predicted by the number of ducks a raptor could force to take flight in one single flyover (i.e. the number of potentially vulnerable ducks, equivalent to prey patch size in this context), rather than the total number of individuals present on the waterbody.

We monitored Teal *Anas crecca* numbers, the frequency of flyovers by Marsh Harriers, and the number of Teal taking flight each time a Marsh Harrier flew over, on a 16 ha waterbody of the Marais du Vigueirat in the Camargue, southern France (43°40′N, 04°38′E). The analysis was restricted to Teal because this is the main dabbling duck present at this site (about 300 individuals on average) and, as it is the smallest of all European dabbling ducks, it is also the species that is most at risk from predators (Guillemain *et al.* 2001) and therefore the most likely to take flight during Marsh Harrier flyovers (M. Lepley & M. Guillemain, pers. obs.). Other dabbling ducks present at this waterbody are mainly Mallard *A. plathyrhynchos* and Shoveler *A. clypeata* (about 150 and 100 individuals on average, respectively; G. Massez, unpubl. data.).

Observations were carried out by the same two observers (M.G. and M.L.) on one day per week from 3 October 2002 to 5 March 2003 and from 1 October 2003 to 3 March 2004, except when meteorological conditions made it impossible (three times in 2002–03, and three times in 2003–04); there were therefore 40

different observation days. During each observation day (generally from around 09:00 to 17:00 hours, or part of that day), all flyovers by Marsh Harriers were recorded (other birds such as Yellow-legged Gulls *Larus cachinnans* and Peregrine *Falco peregrinus* also disturbed the ducks occasionally, but are not considered here), and the number of Teal taking flight was noted each time the Harrier passed above the flock. Observation periods for Marsh Harrier flyovers lasted from 1.5 to eight hours in a day, and daily rate of flyovers (flyovers/min) was then computed. In addition, the total number of Teal present was recorded throughout daylight hours every 60 to 90 minutes.

In order to allow comparison with Fritz *et al.*'s (2000) study, we first tested the relationship between the maximum number of Teal present (considered here on a daily basis), daily average wind velocity (four classes, from 0 = no wind to 3 = strong wind), month of observation, year of observation and the frequency of Marsh Harrier flyovers using backward stepwise general linear modelling (GLM) (threshold *P*-value at 0.05). Daily maximum number of Teal was used instead of daily average, because some birds were sometimes hidden behind vegetation during counts. As in Fritz *et al.*'s (2000) study, the number of Teal and the frequency of flyovers were square-root transformed to normalize the data (Kolmogorov–Smirnov tests: number of Teal: $d = 0.1235$, $P > 0.05$; Marsh Harrier flyover frequency: $d = 0.1257$, $P > 0.05$).

We then performed the same analysis with the maximum number of Teal forced to take flight by Marsh Harrier in a flyover that day instead of the number of Teal present, in order to assess which of these two variables better predicted Marsh Harrier activity. The data were square-root transformed (Kolmogorov–Smirnov tests: number of Teal taking flight: $d = 0.1270$, $P > 0.05$).

Finally, we assessed the relative importance of the number of Teal present relative to the number of Teal taking flight in explaining the variance in Marsh Harrier flyover frequency. Because the two Teal variables were interrelated ($r^2 = 0.58$, df = 38, $P < 0.0001$) they were both entered into a single GLM model and their partial *F*-values compared.

When including the number of Teal present at the site in the GLM analysis, this was the only variable to remain at the end of the backward stepwise procedure ($F_{1,38} = 20.02$, $r^2 = 0.34$, $P < 0.0001$, slope of the relationship + 0.0050 ± 0.0011 se; Fig. 1a), while the effects of wind, month, year or interactions were not significant. When the maximum number of Teal that
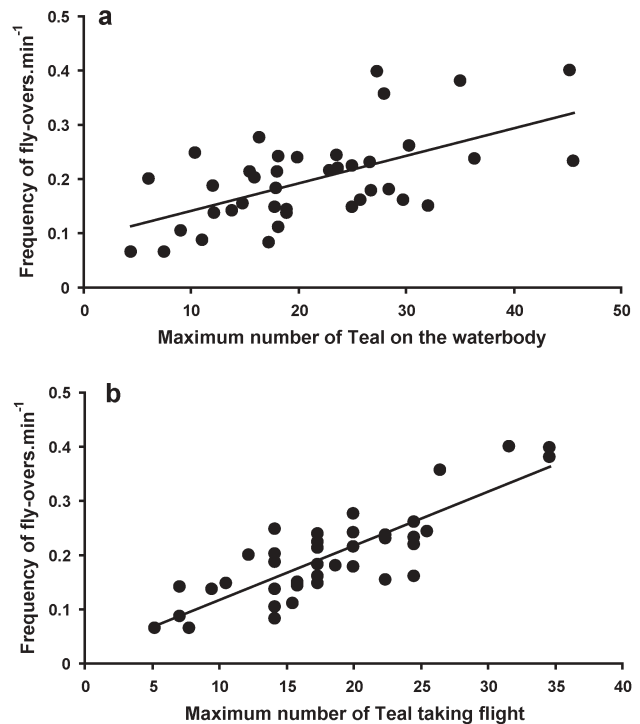

Figure 1. Relationship between the mean daily rate of prospecting flyovers by Marsh Harriers (flyovers/min) and (A) the maximum number of Teal recorded on the waterbody that day ($y = 0.0050x + 0.0915$) and (B) the maximum number of Teal that took flight because of the flyovers that day ($y = 0.0099x + 0.0175$). Rate of raptor flyovers and Teal numbers are square-root transformed.

took flight because of a Marsh Harrier were considered instead, this too was the only variable to remain at the end of the stepwise procedure, but more than twice as much of the variance in frequency of flyovers was explained ($F_{1,38} = 88.91$, $r^2 = 0.70$, $P < 0.0001$; Fig. 1b). When the maximum number of Teal present on the waterbody and the maximum number of Teal taking flight were simultaneously considered, only the latter variable had a significant effect on the frequency of flyovers by Marsh Harriers (Present: partial $F = 0.6881$, $P = 0.4121$; Taking flight: partial $F = 45.44$, $P < 0.0001$).

As in the analysis by Fritz *et al.* (2000) in western France, we found a significant positive relationship between the frequency of prospecting flyovers by Marsh Harrier and the number of Teal present on the waterbody. Interestingly, the slopes were of the same order of magnitude in the two studies (i.e. 0.0018 and 0.0013 in the two sets of sites in western France, 0.0050 here), and similar proportions of the variance in the frequency of flyovers were explained (i.e. 31% for Fritz *et al.* versus 34% in this study). However, and as

expected, the relationship was stronger with the maximum number of Teal taking flight due to Marsh Harriers, as more than twice the percentage of the variance was explained. Marsh Harriers thus seem to use the number of ducks they can get to take flight in one flyover to decide whether to prospect a wetland or not, rather than the total number of ducks they can see on the waterbody. This seems a better measure of their potential benefit given that Marsh Harriers rely on surprise and not all the birds on such a large waterbody can be forced to take flight in one prospecting flyover (other ducks will swim away and not be attacked).

The daily average number of Teal taking flight upon appearance of a Marsh Harrier was more strongly correlated with the maximum number of Teal taking flight at a Harrier flyover than with the maximum number of Teal present that day at the waterbody (r^2 = 0.75 and 0.48, respectively; in both cases df = 38 and P < 0.0001), suggesting that maximum flying group size was a better predictor of potential success for the Harrier than the average number of birds present in total in the area. In addition, it may be difficult for a raptor to determine how many Teal in total are present at a waterbody when the banks are partially hidden by vegetation (as is the case here with *Tamarix* trees). It is likely that Marsh Harriers rely on their own earlier experience, or on information gained from other Harriers (e.g. visual perception of how many ducks other raptors manage to put to flight) to determine the expected number of Teal they will manage to force to take flight.

The benefits for an individual of joining a group, in terms of reducing its own predation risk (through dilution and confusion effects) (Hamilton 1971, Pulliam 1973, Cresswell 1994) or vigilance time (Powell 1974, Bertram 1980, Roberts 1996), are well known. However, the attraction of predators is often considered a drawback of flocking from the prey species' point of view (Krebs & Davies 1993). In the case of dabbling ducks, the diurnal concentrations of individuals seem to attract more predators; the increased presence of predators may therefore limit the behaviour of ducks to low-risk behaviours (e.g. preening instead of foraging underwater) in large flocks, or force them to interrupt their activities more often for vigilance. However, if the number of ducks that can be disturbed in one flight is more important for the predator than the total number of ducks present, then Anatidae may be able to mitigate the costs of

flocking at a site by distributing themselves in a way that keeps their vulnerability to surprise to a minimum.

ACKNOWLEDGEMENTS

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