Pursuit flights of Mallard and Gadwall under different environmental conditions

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The function of pursuit flights in dabbling ducks has promoted a strong discussion (Hori 1963; McKinney 1965). The main controversies concerned whether these flights had a sexual or a territorial function.

Recent evidence shows that for some species the main function of such flights is territorial (e.g. Siegfried 1968, Seymour 1974a, 1974b, Skead 1977, McKinney *et al.* 1978, Seymour & Titman 1978), but for others they have mainly a sexual significance (e.g. Derrickson 1978, Titman & Seymour 1981). However, in recent years it has become apparent that there is no one single function of pursuit flights, and that their significance, at least for some species, changes as the breeding season progresses.

Since pursuit flights act to disperse breeding pairs in relation to available feeding areas (McKinney 1965, Seymour 1974b), ducks might respond to different environmental conditions by means of this territorial behaviour. In this paper some evidence supporting this view is presented for the Mallard *Anas platyrhynchos* and the Gadwall *A. strepera*. Some characteristics of the breeding ecology which can be related to aspects of the pursuit flights are also briefly discussed.

Study area and methods

This study was carried out during the 1977 and 1978 breeding seasons in the Biological Reserve of Doñana and in the Guadiamar Reserve, both within the limits of the Doñana National Park in southwestern Spain.

A detailed description of the Biological Reserve can be found in Allier *et al.* (1974); the main wetland types are the lagoons and the western edge of the Marismas (marshes) of the Guadalquivir River. The Guadiamar Reserve was described by Amat (1980); this area is a saltmarsh situated in the centre of the Marismas.

Because of the winter rains the wetlands of the study area are periodically flooded in most years. However, owing to high temperatures and lack of rain these wetlands dry up in summer, water remaining during this season only in lagoons of the Biological Reserve and in zones of the Biological and Guadiamar Reserves which some years are artificially flooded.

The size of flooded areas remained constant during January-May 1978. In March 1977 the size of flooded area was similar to that recorded during 1978, but due to the lack of rains a 4% loss of flooded areas was recorded between March-April 1977, and an additional 16% loss between April-May 1977 (Amat 1981).

Observations of ducks were made from several vantage points. All the recorded flights of both species were allocated to one of the following categories: a) lone females, b) lone males, c) a pair, d) two males chasing a female, e) three males chasing a female, f) four males chasing a female, and g) more than four males chasing a female. Pursuit flights can be distinguished as three bird flights and attempted rape flights (McKinney 1965), but for the purposes of this study they are considered together, unless otherwise indicated.

Results

In the Marismas Mallard start showing antisocial behaviour from November-December when break-up of flocks occurs, while for Gadwalls this takes place from January-February. For the two species the most frequent type of pursuit flight is that involving three birds (Table 1). As the breeding season progresses lone drakes are observed more often, and in fact there is a close relationship between the observed proportion (arcsin $\sqrt{p_i}$ transformed) of lone drakes and that of pairs for both Mallard ($r = -0.996$,

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Table 1. Number of different flight categories recorded during the 1977 and 1978 breeding seasons, the two years combined.

Flight category	Species	Jan	Feb	Mar	Apr	May
A	Lone female					
	Mallard	0	2	21	5	6
	Gadwall	0	0	3	2	2
B	Lone male					
	Mallard	6	8	263	414	448
	Gadwall	0	0	3	11	26
C	Pair					
	Mallard	33	101	388	103	74
	Gadwall	0	0	111	158	48
D	2 males/female					
	Mallard	4	5	68	13	10
	Gadwall	0	0	11	18	9
E	3 males/female					
	Mallard	0	0	21	8	4
	Gadwall	0	0	5	6	3
F	4 males/female					
	Mallard	0	0	3	2	0
	Gadwall	0	0	0	4	0
G	> 4 males/female					
	Mallard	0	0	11	8	5
	Gadwall	0	0	1	2	5

N = 5, $P < 0.01$) and Gadwall ($r = -0.999$, N = 3, $P < 0.05$), as could be expected from the fact that the break-up of pair bonds occurs one or two weeks after the onset of incubation.

For Mallard the greatest proportion of pursuit flights was recorded in March of both years (Figure 1), but it was greater in 1977 than in 1978 ($t_s = 2.91$, P = 0.004). The Gadwall also showed the greatest proportion of pursuit flights in March 1977, but in 1978 this took place in April (Figure 1). Since the greatest frequency of pursuit flights in both species was recorded in 1977 earlier than in 1978, it can be supposed that this was due to the different availability of flooded areas between the years. This could cause territories to be established earlier in 1977 than in 1978.

There exists some evidence indicating that the more crowded the population, the more frequent the pursuit flights (Duebbert 1966). The number of pursuit flights/day of observation is used as a measure of the frequency of pursuit flights. The density of breeding populations is the number of ducks/ha of flooded area (Amat 1981). To avoid the effects of break-up of pair bonds only the corresponding figures for March are considered, because after that month a great proportion of females are incubating or with ducklings (Amat 1982). The result (Table 2) indicates that there does seem to be some relationship between the density of breeding populations and the frequency of pursuit flights.

Table 2. Relationship between the density (ducks/ha) of breeding populations and the frequency of pursuit flights during March 1977 and 1978.

	1977	1978
Mallard		
Density	0.35	0.32
Flights/day	8.6	6.8
Gadwall		
Density	0.10	0.13
Flights/day	1.2	1.5

As the breeding season progresses pursuit flights turn into attempted rape flights. These are characterized by a greater number of pursuers and are more vigorous and long-lasting than typical three bird flights (Dwyer 1974, Titman & Seymour 1981). As shown in Table 3 the number of pursuers of a female in-

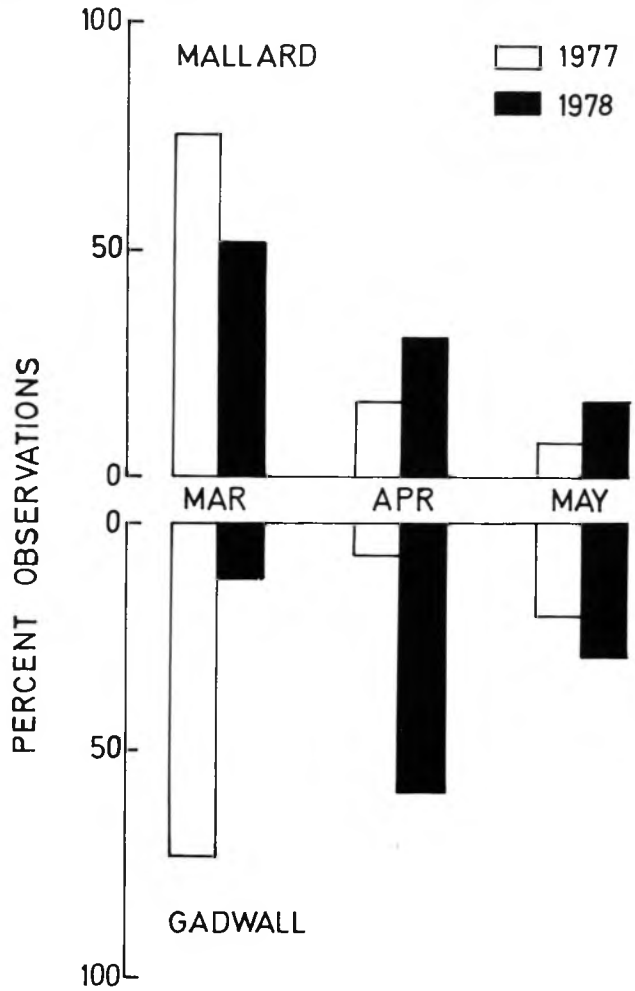

Figure 1. Percentage distribution of pursuit flights during March-May 1977 and 1978 for Mallard (N = 101 and 52, respectively) and Gadwall (N = 15 and 49).

Table 3. Mean number of pursuers of a female during the 1977 and 1978 breeding seasons, the two years combined. Sample size in parentheses.

Species	Jan	Feb	Mar	Apr	May
Mallard	2.0 (4)	2.0 (5)	2.9 (103)	5.0 (31)	4.7 (19)
Gadwall	–	–	2.6 (17)	3.0 (30)	3.8 (17)

would prove unsuccessful, and the female could be reached and mounted repeatedly by her pursuers. In the Marismas, the more vigorous attempted rape flights were recorded at the end of the breeding season (up to 19 Mallard males and up to 13 Gadwall males chasing creases throughout the breeding season. Females chased by several males evade their persecution by diving and hiding in dense emergent vegetation (Skead 1977, Bailey *et al.* 1978, Titman & Semour 1981). However, over habitats with shallow water, this means of evasion

a female), when most wetlands of the study area had a water depth of less than 0.3 m.

In May of both years up to 10 dead Mallard females were recorded, their heads and backs without feathers and completely bloody. Some females still alive were in the same condition and flew with difficulty, showing a very secretive behaviour. This suggests that they were hiding from males and also that they could be very vulnerable to predators. Only one dead Gadwall female was found in such a condition. These observations suggest that all such females were repeatedly mounted by several males, causing their deaths.

Discussion

In 1977 Mallard started laying three weeks earlier than in 1978, this difference being less obvious for Gadwall (Amat 1982). A certain synchronization between laying dates and available food for ducklings must exist (Hildén 1964). An earlier reduction in the size of the flooded areas could motivate an earlier onset of laying to allow the complete development of ducklings. Because nest site selection takes place only some days before laying and the males of both species spend a great proportion of time on territories, the lag in the frequency of pursuit flights between 1977 and 1978 is not surprising. The greater number of pursuit flights is recorded precisely during the nest initiation period (Stewart & Titman 1980).

A greater extent of flooded areas could attract a greater quantity of breeding pairs (Weller 1979; Amat 1981; Godin & Joyner 1981). Since the pursuit flights serve to space out the pairs, the females avoiding areas from which they were chased, this mechanism could contribute to regulate breeding duck populations in relation to available flooded areas. This must be very important in a region such as that studied in which the flooded area is drastically reduced in late spring and early summer. By means of this spacing mechanism high duckling densities in reduced areas could be prevented, and hence intraspecific competition minimised (cf. Dzubin 1969; Patterson 1976). Also, as the nests are more spaced out, predation would be lowered.

As the breeding season progresses there is an increasing surplus of lone drakes, which begin to integrate in small flocks. Late in the breeding season birds of these flocks will pursue either lone or paired females (Bailey *et al.* 1978). The aim of these pursuits seems not to be territorial, but rather sexual since all males attempt to rape the female (Titman & Seymour 1981). It has been suggested that the individuals performing this rape would increase their reproductive fitness, since the female would be fertilized by them. However, as I have suggested the rape of a female by several males could cause her death, and thus the individual fitness would not always increase.

Stewart & Titman (1980) and Titman & Seymour (1981) pointed out the benefits of the pair bond to both male and female. Males of species having weak territorial systems spend less time on their territories until the break-up of pair bonds, and also employ a more promiscuous strategy than do strongly territorial ones. The proportion of time spent on territories could be explained if the uncertainty of habitats is considered (Orians 1973; Pitelka *et al.* 1974). At least for Pintail *Anas acuta* and Mallard there exists some evidence indicating that the former species (the less territorial) breeds in more unpredictable areas (Calverley & Boag 1977). It would be adaptive to employ a more mobile strategy to track the more profitable environmental patches (Gardarsson 1979; Amat 1980; Herrera 1980; Kaminski & Prince 1981). This mobility would prevent males from making an efficient defence of their mates, and therefore they might employ a more promiscuous strategy, rewarded by an increase of their reproductive fitness. Since the home range of these species is greater than that of strongly territorial ones (see Derrickson 1978), it would be difficult for a female to find her mate when moving from the nest to the feeding area. Hence, the benefit for such a female to be mounted by other males than her own seems obvious.

Among dabbling ducks, Shoveler *Anas clypeata,* Blue-winged Teal *A. discors,* Gadwall, Black Duck *A. rubripes,* Mallard and Pintail show progressively a more or

less strongly territorial behaviour (Titman & Seymour 1981). The same specific ranking is more or less maintained when distance from nest to water is considered, the more territorial species nesting nearer to water. The more territorial species defend feeding areas and the surroundings of nest site against conspecifics (Seymour 1974b, Stewart & Titman 1980), while the weaker territorial ones defend only feeding areas (Seymour & Titman 1978). Thus, the distance from nest to water seems to be an important ecological trait resulting from different territorial tactics. With a nest located away from water it would be impractical to defend the surroundings of nest site, because in the absence of the male from the feeding area this could be occupied by another pair. However, if the nest is close to water the male would become aware of intrusions into the feeding area, even if he were on the nest site. He could move immediately towards intruders to drive them off. This tactic would allow a strongly territorial male to stay for prolonged periods near his mate, and in this way he could prevent other males from mounting her. By doing so such a male would protect his reproductive investment, otherwise difficult to assure.

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Summary

The pursuit flights of Mallard *Anas platyrhynchos* and Gadwall *A. strepera* were recorded in the Marismas of the Guadalquivir (southwest Spain) during the 1977 and 1978 breeding seasons. The size of flooded areas was greater in 1978 than in 1977. As a result, the greatest frequency of pursuit flights was recorded in 1977 earlier than in 1978 for both species. There seems some relationship between the density of breeding populations and the frequency of pursuit flights. The number of pursuers of a female increased throughout the breeding season. By the late breeding season some females were found dead, apparently raped by several males. The role of pursuit flights as a mechanism helping to regulate breeding dabbling duck populations in relation to different availability of flooded areas is discussed. Some characteristics of the breeding ecology of dabbling ducks can be related to aspects of the pursuit flights.

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