Infertile eggs: a reproductive cost to female dabbling ducks inhabiting unpredictable habitats

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Holarctic dabbling ducks (genus *Anas*) are primarily monogamous, although a variable degree of promiscuity exists in most species (McKinney *et al.* 1983; McKinney 1985). Pairs space out during breeding, maintaining an 'activity centre' where females feed undisturbed and copulate (Seymour 1974). The primary spacing mechanism is the pursuit flight, since the females avoid areas from which they have been chased (Smith 1968). Because females probably choose the activity centres, the target of pursuer males is frequently the female of an intruding pair (Titman and Seymour 1981). After a chase, the pursuer male quickly returns to the activity centre, apparently to avoid the possibility of harassment (and perhaps cuckoldry) of his mate by other males. This is important so that the female can feed undisturbed as long as possible during the laying period; also, the female benefits from male surveillance as this may reduce the risk of predation (McKinney 1973). Spacing behaviour may also result in minimised intraspecific competition for food at the activity centre (Dwyer 1974).

In a comparative study of pursuit flights, Titman and Seymour (1981) concluded that Shoveler *A. clypeata*, Blue-winged Teal *A. discors*, Gadwall *A. strepera*, Black Duck *A. rubripes*, Mallard *A. platyrhynchos* and Pintail *A. acuta*, show a continuum of decreasing territorial behaviour. Species with strong territorial behaviour spend more time on territories and are less promiscuous than weakly territorial species. The proportion of time spent by males on territories is related to the variablility of habitats, and therefore food availability (Derrickson 1978; Titman and Seymour 1981; Nudds and Ankney 1982).

Because dabbling ducks that inhabit the more variable environments employ a mobile strategy to track profitable environmental patches, it has been suggested that this would incur some costs to the females of the less territorial species. Frequent mobility might prevent males from efficiently guarding their mates (Amat 1983). Davies (1985) gives evidence for this in a small passerine. When females move and their mates are absent, they could be pursued and mounted by other males (Stewart and Titman 1980). Also, in the weakly territorial *Anas* species the break-up of pair bonds occurs during the first or second week of incubation, in the strongly territorial ones during the third or fourth week (Titman and Seymour 1981). However, the males of the less territorial species begin to congregate in small flocks even before the break-up of pair bonds. It has been suggested that these unemployed males seem to wait for females to return from their nests to join their mates, so that when the female arrive near the group, the males chase them attempting forced copulations (McKinney 1973; Derrickson 1978; McKinney *et al.* 1983). Females involved in forced copulations may be injured or killed by the pursuer males (Smith 1968; Amat 1983; McKinney *et al.* 1983).

In this paper the potential reproductive cost to female dabbling ducks in relation to territorial systems and habitat characteristics is addressed.

The number of males pursuing single females may be considered as an index of the potential risk of injury incurred by females. When a chase is in progress, more and more males join it. Therefore, it should be adaptive for females to submit to forced copulations once a chase has been initiated, since 'the faster the event is concluded the less chance there is of additional males joining it' (McKinney *et al.* 1983). However, this would not be adaptive late in the season because of the tendency of the males to be in flocks. Females should therefore try to escape from pursuers, and the egg may remain unfertilised if they are successful in escaping.

In the marshes of the Guadalquivir River (SW Spain) the size of the flooded area decreases throughout the breeding season. There male Mallards were observed to congregate in small flocks as the breeding season progressed, and the number of males pursuing single females increased throughout the season. By the late breeding season some females were found dead, apparently as a result of forced copulations

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by several males (Amat 1983).

As the risk of injury for females increased throughout the breeding season, so did the proportion of nests with infertile eggs. A test of equality of proportions shows that infertility in early clutches (0 of 10) is significantly less than in mid (4 of 32) or late (4 of 13) clutches. However the difference between mid and late clutches is not significant, probably because of the small samples. The trend is consistent with the hypothesis (Koenig 1982) that 'increased competition for mates and/or intrasexual competition during egg laying leads to greater interference and a lower probability that eggs will be fertilised'. Given the variation in mobility among species (see above), it might therefore be that the same trend was apparent at the interspecific level of comparison.

Extensive search of the literature for information on the frequency of infertile eggs in successful waterfowl nests revealed few studies reporting such data. An analysis was restricted to four of the six species considered by Titman and Seymour (1981) because very few data were available for the other two. Only those studies were considered in which unhatched eggs were examined to differentiate between embryonic deaths and infertility. Within the category of eggs termed 'infertile' there could have been some with early embryonic deaths (see Munro and Kosin 1945), but there was no way to check for this.

Females of duck species with weak territorial behaviour had a greater proportion of infertile eggs in nests than did the more strongly territorial species (Table 1; χ^2= 23.0, $P<0.001$). Due to costs incurred by females in the production of eggs it may seem surprising that some of the eggs will not be fertilised. Therefore either females have other potential costs greater than leaving some eggs unfertilised or eggs are not nearly so 'costly' as often is assumed. Anyway, this evidence supports the idea that the more promiscuous *Anas* species, which occupy more variable habitats, lay a greater proportion of infertile eggs than the less promiscuous species.

Table 1. Frequency of infertile eggs in successful nests of four dabbling duck species, which are ordered as increasing the degree of territoriality, following Titman and Seymour (1981), from top to bottom of the table. Source: Girard (1941), Miller and Collins (1954), Hunt and Naylor (1955), Steel *et al.* (1956), Rienecker and Anderson (1960), Ogilvie (1964), Duebbert (1966), Bengtson (1972), Amat (1982), and Hines and Mitchell (1983).

Species	Number of eggs examined	Percentage of infertile eggs
Pintail	2946	3.3
Mallard	12055	2.3
Gadwall	15442	2.2
Shoveler	1479	1.1

Although duck females are known to store viable sperm up to 17 days (Elder and Weller 1954; Burns *et al.* 1980), the summarised information of Table 1 suggests that for wild ducks the period of sperm viability seems not to be long enough for a complete clutch to be fertilised. Perhaps, the period of sperm viability may be longer for females of the less territorial species because of the greater difficulty they apparantly have of meeting their mates (cf. Hatch 1983). In spite of this, the mechanism does not appear to be effective enough in dabbling duck females of the less territorial species to prevent an increase in egg infertility.

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Summary

For a female dabbling duck, the risk of being involved in forced copulations increases throughout the nesting season. This risk is greater for less territorial species occupying more unstable habitats. A potential consequence of forced copulations is that the female can be injured or killed. Species inhabiting the more unstable habitats lay more infertile eggs than those living in more stable habitats, perhaps because if females escape from pursuer males the egg will not be fertilised.

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