Persistent quacking in dabbling ducks: a predator-luring signal?

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Female dabbling ducks of many species give bouts of loud, monotonous quacks during the pre-laying period. From their characteristics, and the situations in which they are given, these calls do not appear to be directed towards the mate or other conspecifics. Persistent quacking is closely associated with nest-site prospecting and it can be triggered by various stimuli, including the appearance of potentially dangerous predators. We suggest that this vocalization is designed to attract the attention of mammalian predators, causing them to betray their presence. The information obtained could be valuable to females in enabling them to select safe nest-sites.

Many species of birds and mammals respond to the sight of a potential predator by giving conspicuous vocal or visual signals. In some species, these signals apparently function primarily to warn conspecifics (e.g. Sherman 1977) but in other species they are directed at the predator itself. Recent discussions of "tail-flagging" and "stotting" in ungulates (Smythe 1970, 1977, Bildstein 1983, Caro 1986 a,b, Fitzgibbon & Fanshawe 1988) and tail-flicking in Eastern Swamphens *Porphyrio porphyrio* (Woodland *et al.* 1980, Craig 1982) suggest that these conspicuous signals may have been designed to inform predators that they have been seen.

During the early part of the breeding season, female Mallard *Anas platyrhynchos* give extended bouts of quacking (Lorenz 1941, Hochbaum 1944, Dzubin 1957, Abraham 1974, Caldwell & Cornwell 1975) and similar calling has been recorded in many other dabbling ducks. This "persistent quacking" (PQ) raises two main questions: who is the intended receiver of the call, and how do individual females benefit by calling? In this paper we present observational evidence on the first of these questions.

Three types of recipient for PQ have been proposed:

(1) The female's mate. Hochbaum (1944) thought that the calls announce the female's choice of a breeding place and stimulate her mate to defend it. McKinney (1975) suggested that the calls ensure that the female's mate stays close to her during nest-site prospecting, providing vigilance for predators while she explores nesting cover.

(2) Conspecific pairs. Abraham (1974) suggested that the calls discourage other pairs from intruding in the territory and thereby promote spacing out of nests, reducing the risk of predation. Dzubin (in Palmer 1976) also thought that PQ functions in the spacing of pairs.

(3) Predators. McKinney (1975) suggested that the calls lure predators, making them reveal their presence, and that the information gained subsequently influences the female's choice of a nest-site.

It is possible that PQ serves two or more of these functions, and/or perhaps other functions not yet envisaged. To set the stage for experimental testing of hypotheses, and to draw attention to what may be a novel anti-predator tactic, we review available evidence on the characteristics of the calls, the contexts in which they are given, and the responses of potential recipients to them. Similar calls are given by some dabbling ducks at other stages in the annual cycle (McKinney 1970, Abraham 1974, McKinney *et al.* 1978) but here we are only concerned with the early part of the breeding season.

Methods

The observations on captive ducks were made in two adjacent flight pens, each measuring 27.5 x 27.5 x 3.6 m (McKinney 1967). Eight pairs of full-winged, wild-caught Green-winged Teal *Anas crecca carolinensis* were observed

from 26 April to 30 June 1973, usually for 3 h, on two of every three mornings starting at first light, and from dawn to dusk on 9 May and 25 May (McKinney & Stolen 1982). Eight pairs of Mallards were studied in these pens in 1978 (Burns *et al.* 1980, Cheng *et al.* 1982, 1983). Observations on breeding pairs of wild-caught Northern Pintail *A. acuta* (Derrickson 1977), Cape Teal *A. capensis*, and Red-billed Pintail *A. erythrorhyncha* and on captives obtained from aviculturists in the USA of White-cheeked (or Bahama) Pintail *A. bahamensis* and Chilean Teal *A. flavirostris* were also made in the same flight pens in other years. The captive birds were individually marked with coloured and/or numbered nasal discs or saddles.

Field observations on unmarked wild birds (mainly Mallard and Green-winged Teal) were made near Pine Lake, 34 km southeast of Red Deer, Alberta (113°20'W, 50°N), in an area of rolling parkland and pastures dotted with many small, wooded potholes, from 18 April to 12 June 1976 and 21 April to 29 June 1977. Cape Shovelers *A. smithii* were observed (by FM) at Mossel Bay, Cape Province, South Africa in mid-July and late August 1968, near the estuary of the Little Brak River. Wild Northern Pintails were observed (by SRD) near Medina, North Dakota during three breeding seasons (1971-73).

Results

Characteristics of PQ calls

In the Mallard, PQ consists of loud single notes, repeated regularly at a rate of about 2 per s, in bouts lasting up to several minutes. Samples from four captive Green-winged Teal females gave means (±s.e.) of 15.13 ± 0.78 (n = 105), 5.47 ± 0.64 (n = 34), 8.00 ± 1.29 (n = 12), and 8.27 ± 1.75 (n = 11) notes per bout. Females often give bout after bout, sometimes for several hours. Apart from the Northern Shoveler *A. clypeata*, in which each note is usually two-syllabled, PQ is very similar in all other species of *Anas* we have studied.

Spectrographic analyses of the calls of Mallards (Abraham 1974) and Northern Pintails (Derrickson 1977) showed that individual notes begin and end abruptly, and are relatively consistent in duration, amplitude, frequency, and interval. These structural characteristics make PQ easy to locate and suggest that PQ is designed primarily to draw attention to the caller. Like the advertising calls of crickets, cicadas, and frogs, PQ may serve as a broadcast signal (Marler 1959).

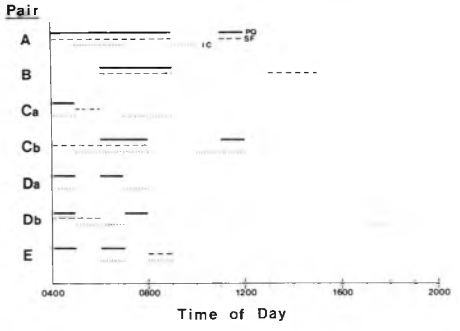

Figure 1. Occurrence (1 or more bouts/hr.) of persistent quacking (PQ), spontaneous flights (SF), and inspecting cover (IC) by pre-laying females during all-day (dawn to dusk) continuous watches in flight pens. (A, B) Green-winged Teal females Y1 and G1, 9 May 1973; (Ca, Cb) Mallard female EB on 17 May, 3 June 1978; (Da, Db) Mallard female EG on 17 May, 3 June 1978; (E) Mallard female WG, 3 June 1978.

Time of day

In Mallards, PQ is heard mainly in morning and evening twilight periods (Dzubin 1957) but is especially frequent shortly before and after dawn (Hori 1963, Abraham 1974). In captive Green-winged Teal and Mallards, PQ was recorded mainly during the first 5 h after dawn (Fig. 1) and in wild Green-winged Teal, most records of PQ were in the morning hours (80% of 51 in 1976; 77% of 30 in 1977). We have noted similar tendencies also for other *Anas* species. This is the time of day when nest-sites are selected and eggs are laid.

Associated behaviour

Persistent quacking is especially characteristic of the beginning of the breeding season (Hochbaum 1944, Dzubin 1957, Hori 1963). Dzubin (in Palmer 1976) noted Mallards searching nesting cover on foot 5-10 days after PQ started and, in warm springs, laying began 4-5 days later. A close relationship to the pre-laying phase was confirmed for individual females of known breeding status in flight pen studies on Northern Shoveler (McKinney 1967), Mallard (Fig. 2 and Abraham 1974), Northern Pintail (Derrickson 1977) and Green-winged Teal (McKinney & Stolen 1982). In these species, most PQ was heard from females during the ten days before laying began, but some individuals started calling earlier (23-24 days in

Northern Shoveler, 18 days in Northern Pintail). Most females stopped calling abruptly when they began to lay, but a few continued to call for 1-4 days (one of 12 Mallards, one of six Northern Shovlers, one of seven Northern Pintails).

Persistent quacking has been recorded also before renesting attempts in captive Green-winged Teal (McKinney & Stolen 1982), Mallards (Fig. 2), and White-cheeked Pintails (unpublished data) but the period of calling was much shorter (one or a few days) than before initial nesting attempts.

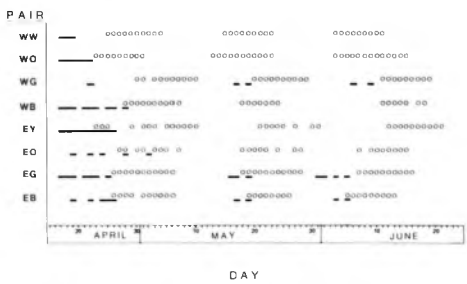

Figure 2. Incidence of persistent quacking (bars) in relation to laying dates for first clutches and two replacement clutches (circles) in eight Mallard females. In this 1978 flight pen study, clutches were removed when complete to induce females to renest.

An early indication of nest-site selection behaviour in dabbling ducks is the occurrence of low, slowly-paced flights by pairs over areas that include potential nesting cover (Hochbaum 1944, Sowls 1955, Dzubin 1955, 1957, McKinney 1965, Smith 1968, Skead 1976). Persistent quacking commonly occurs before and during these flights which are initiated and led by the female. Calling females often assume an alert posture with head erect, and then change location between calling bouts, either by swimming from one part of a pond to another or by flying to another pond or to an adjacent upland area. In captives of all *Anas* species studied, exploring cover and spontaneous flights around the pen by the pair or the female alone were closely associated activities (Fig. 1). After one or a series of flights, often accompanied by PQ, females then became silent and walked into long grass where they explored for nest-sites. Repeated calling by female ducks was noted by Lorenz (1941) to precede a move to a different place and he interpreted this "departure call" as a signal indicating flight intention.

Relationship to the mate

Both Dzubin (1957) and Abraham (1974) noted that PQ is given by female Mallards whether or not the mate is present and they did not report males responding to the calls of their mates. In dabbling ducks, the usual female contact call, given when mates become separated, is the decrescendo call (Lorenz 1941). Males recognize their mates individually by this call and typically they respond by rejoining the female (Lockner & Phillips 1969, Abraham 1974). In wild Green-winged Teal we recorded PQ most often from females accompanied by their mates (n = 68), although sometimes the male was absent (n = 6). We noted no obvious differences in the quality of the calls in the latter situations. In all species studied in flight pens, males were almost always nearby while their mates were making flights, giving PQ, and exploring cover. In fact, males tend to guard their mates especially closely during the pre-laying period when extra-pair copulations can lead to fertilization of eggs (Burns *et al.* 1980, McKinney *et al.* 1983, Evarts & Williams 1987). These observations suggest that PQ is not primarily designed to maintain contact between mates in these species.

Stimuli apparently triggering PQ

Bouts of PQ often begin spontaneously without any apparent environmental stimulus. Calling can also be elicited by disturbances of various kinds. For example, we have induced PQ by "peeking" (briefly showing the top half of our heads) over the perimeter fence of flight pens containing breeding pairs of Cape Teal, Chilean Teal, Northern Pintails, and White-cheeked Pintails. One female Chilean Teal, which was in the pre-laying phase and had been giving many PQ bouts on previous days, responded promptly by approaching and starting PQ. When we moved around the outside of the pen, showing ourselves partially from time to time, this female (followed by her mate) approached us repeatedly, while continuing to give PQ. Similar approach+inspect+PQ responses to humans were observed in wild Green-winged Teal, Mallard, Northern Pintail, Blue-winged Teal *A. discors*, and Gadwall *A. strepera* (Table 1).

As Abraham (1974) noted in Mallards, PQ seems to be infectious. In both captive and wild Northern Pintails, especially at twilight periods or after an alert, when one female started calling other females often approached the calling bird and then began giving PQ.

We conclude that PQ is, to some degree, influenced by environmental stimuli. In particular it can be triggered by the appearance of

Table 1. Examples of stimuli that trigger persistent quacking in dabbling ducks.

Stimulus	Circumstances	*Anas* Species
Humans		
(a) In view but distant	Pre-laying period, especially at dusk	*clypeata, smithii*
(b) Approaching pond in full view	Early breeding season, when pair flies up	*platyrhynchos, crecca, acuta, discors, strepera*
(c) Close to pond, partly concealed	Pre-laying period, when female swims up to or flies over person apparently to inspect visually	*platyrhynchos, crecca, acuta, discors, capensis, strepera, flavirostris*
Sudden noise	Early breeding season, when tractor started, cardoor slammed, dogs barking, beaver felled tree splashed into pond	*platyrhynchos, acuta, strepera*
Domestic dog (*Canis familiaris*)	Early breeding season, when pair swims toward dog running along edge of pond	*acuta*
Red fox (*Vulpes fulva*)	Pre-laying period, when pair alert swimming toward fox moving across field near pond	*acuta*
Crocodile (*Crocodylus niloticus*)	Breeding season, when pair swam along close to a surface swimming crocodile	*sparsa*
Northern Harrier (*Circus cyaneus*)	Pre-laying period, when harrier flew over flight pen and 3 pairs became alert and swam to center of pond	*crecca*

a potential predator, a sudden noise, or the PQ of nearby females (Table 1).

Comparative evidence

In addition to the nine *Anas* species already mentioned (Mallard, Green-winged Teal, Northern Pintail, White-cheeked Pintail, Northern Shoveler, Chilean Teal, Cape Teal, Gadwall, and Blue-winged Teal) PQ during the pre-laying phase has been reported also in North American Black Duck *A. rubripes* (Seymour & Titman 1979), Cape Shoveler and Cinnamon Teal *A. cyanoptera septentrionalium* (McKinney 1970), African Black Duck *A. sparsa* (McKinney et al. 1978), and American Wigeon *A. americana* (Wishart 1983). With the addition of our unpublished records for Chestnut Teal *A. castanea*, Chiloe Wigeon *A. sibilatrix*, Silver Teal *A. versicolor*, and Brown Pintail *A. georgica spinicauda* PQ has now been found in 20 of 36 living species of *Anas*. The only exception discovered to date is the Laysan Teal *A. laysanensis* which lives on Laysan Island where there are no mammalian predators. Moulton & Weller (1984) listened for PQ but failed to hear it in two breeding seasons. Loud calls are given frequently by female Maned Geese *Chenonetta jubata* during nest-site selection (Kingsford 1986), and it is possible that other waterfowl have calls that are functionally analogous to PQ.

Discussion

The physical characteristics of PQ suggest that the caller is broadcasting information on her presence and location. The intended receiver is unlikely to be the female's mate because (a) her mate is usually at her side or close by and the calls are unnecessarily loud; (b) calling usually continues despite close attendance by the male; (c) females have other vocalizations for maintaining contact with the mate.

There is no evidence that PQ promotes the spacing out of breeding pairs. PQ occurs in non-territorial species such as the Northern Pintail (Smith 1968, Derrickson 1977) and Green-winged Teal (McKinney & Stolen 1982) as well as territorial species such as the Mallard (Dzubin

1969), Northern Shoveler (Seymour 1974), and Blue-winged Teal (Stewart & Titman 1980). Furthermore, in territorial species we have noted no close temporal relationship between PQ and the expulsion of territorial intruders, nor does PQ seem to have a deterrent effect on intruding pairs.

The close temporal association between PQ and nest-site prospecting, the triggering of PQ by alarming stimuli, and the investigation of the sources of such stimuli by the female suggest that potential predators are the intended receivers. It is well known that dabbling ducks will respond to dogs by swimming toward them and this response has been exploited, using trained dogs, in the ancient duck-catching practice of "decoying" (Payne-Gallwey 1886, McCabe & Mulder 1961). The birds' behaviour is usually considered to be an anti-predator tactic whereby a predator is kept in view and the risk of a surprise attack is reduced. Similar surveillance responses, involving keeping a predator in view by following it, have been reported for various birds and mammals (e.g. Kruuk 1964, 1972, 1976, Walther 1969).

Canids, notably the red fox of Europe *Vulpes vulpes* and North America *V. fulva*, are major predators on dabbling ducks, and it has been shown that nesting females are especially vulnerable (Sargeant 1972, Sargeant *et al.* 1984). Most nest-sites are on the ground, in vegetation, and female ducks frequently feign death when captured by a fox, apparently as an escape tactic (Sargeant & Eberhardt 1975). PQ appears to be another element in the anti-predator strategies of dabbling ducks.

We propose that PQ functions in the detection, luring, and surveillance of predators by female dabbling ducks. Our observations suggest that there are several stages in this process. Initially, spontaneous bouts of PQ attract the attention and stimulate the curiosity of predators such as foxes, causing them to betray their presence to the calling duck. When such a calling bird becomes alerted by a disturbing visual or auditory stimulus in the environment, she continues to call while approaching the source of the stimulus. In this investigative stage, the duck's loud, persistent calls may serve a luring function, causing the predator to emerge from cover and show itself. Once the predator has been detected and sighted, PQ calling continues during the surveillance stage while the duck swims after the predator keeping it in view.

If PQ enables female ducks to detect and monitor the activities of predators within the breeding home range, there could be both short-term and long-term benefits. On an immediate time-scale, females could reduce the risk of surprise attack as they explore cover on foot during nest-site prospecting. More importantly, knowledge accumulated by many such excursions and evaluations could play a key role in the female's decision on where to lay the first egg of her clutch. This decision is very important to a ground-nesting duck because of (a) the risks she will run while visiting the site during laying and while spending most of her time there during the 3-4 weeks of incubation, and (b) risks to her ducklings on their initial trip between the nest-site and a wetland.

In addition to the proposed luring effect, it is possible that PQ has other influences on predators. For example, by exhibiting PQ+approach in response to a predator, that predator is informed that it has been seen and that attempts to catch the duck will be fruitless.

Testing of this hypothesis will require experiments to establish the stimuli eliciting PQ, document the responses of predators to PQ, and determine whether selection of the nest-site is influenced by encounters with predators. Further tests of the hypothesis might come from situations where nesting females are safe from mammalian predators and PQ is absent, as appears to be the case on Laysan Island.

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