

A comparison of pursuit flights by six North American ducks of the genus *Anas*

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Pursuit flights have been recorded in most species belonging to the genus *Anas*. These aerial chases have been called territorial defence flights (Hochbaum 1944), three-bird flights or chases (Dzubin 1957; Hori 1963; McKinney 1965) expulsion flights (Lebret 1961) or *Vertreiben* (Geyr 1929) and attempted rape flights (Lebret 1961) or *Hetzjagen* (Geyr 1929). Controversy has surrounded pursuit flights because of different motivations attributed to participants and because of their difference in form from one species to another.

McKinney (1965, 1975) has reviewed the influence of pursuit flights upon spacing and breeding behaviour in a variety of ducks. Several authors have associated pursuit flights with territorial defence in various members of the genus *Anas* (Dzubin 1957; McKinney 1965, 1975; Titman 1973; Dwyer 1974; Seymour 1974c; Seymour & Titman 1978). The aim of this study was to compare and contrast the pursuit flight component of territorial behaviour in six species of surface feeding ducks: Mallard *Anas platyrhynchos*, Pintail *A. acuta*, Black Duck *A. rubripes*, Gadwall *A. strepera*, Blue-winged Teal *A. discors* and Northern Shoveler *A. clypeata*. Further details on aerial pursuit activity and on the social systems of Black Duck, Mallard, Blue-winged Teal and Shoveler appear elsewhere (Titman 1973; Seymour 1974a, 1974b, 1974c; Seymour & Titman 1978; Stewart & Titman 1980) and results reported here represent a synthesis of new and already reported results.

Study areas and methods

Pursuit flights by six species were observed during intensive breeding biology investigations from 1968 to 1976. The species other than *rubripes* were observed primarily in the pothole country of south-western Manitoba. This area consists mainly of agricultural land dotted with small ponds. Observations were conducted in a region containing 35 to 70 ponds per km², ranging in size from 0.04 ha to 5.0 ha. Detailed

descriptions of this habitat and its waterfowl populations were given by Kiel *et al.* (1972). Observations were also made along a roadside ditch and an adjacent flooded meadow near Delta, Manitoba. This area has been described by Sowls (1955). Observations of *rubripes* were made in a 170 ha cordgrass *Spartina* spp. marsh in a tidal estuary near Antigonish, Nova Scotia. Permanent ponds at the periphery of this marsh ranged in size from 0.6 to 3.8 ha (Seymour & Titman 1978).

Individual *clypeata*, *platyrhynchos*, *discors* and *rubripes* were marked with nasal saddles (Bartonek & Dane 1964) following capture using cannon-nets, baited decoy traps and various nest traps. Peaks of reproductive activity and general progress through the breeding season were apparent from behavioural observations and the results of nest searches in representative locations. Observations and long-range identification of marked individuals were aided by binoculars and 20–45× telescopes. Pursuit flights were timed using stopwatches from the beginning until chasers had abandoned pursuit.

For each pursuit flight observed, the following information was recorded: time, date, weather conditions, location, number and breeding status of individuals involved, duration, height and distance travelled, behaviour, perpetrator and object of behaviour and landing location of participants.

Results

Pursuit flights could generally be classified as Three-bird Flights or Attempted Rape Flights (McKinney 1965). Difficulty arose when Three-bird Flights evolved into Attempted Rape Flights or when numbers involved or behaviour caused confusion. Several characteristics of both types of pursuit flight grouped together are listed and described quantitatively in Table 1. In all species the chasers were always males. Chasing males and chased birds appeared to be paired individuals in most if not all pursuit flights.

Table 1. A comparison of pursuit flight characteristics in six species of *Anas* ducks. Three-bird Flights and Attempted Rape Flights are considered together.

Characteristic	A. <i>acuta</i>	A. <i>platyrhynchos</i>	A. <i>rubripes</i>	A. <i>strepera</i>	A. <i>clypeata</i>	A. <i>discors</i>
Male(s) chasing a female or pair						
% occurrence	100	98.4	99.0	90.2	64.9	46.2
Male chasing male						
% occurrence	0	1.6	1.0	9.8	35.1	53.8
Number involved						
% with 3 or less	66.9	79.0	97.1	82.1	93.0	96.0
% with 4 or more	33.1	21.0	2.9	17.9	7.0	4.0
Aggression between chased male and chaser						
% occurrence	0	1.5	1.2	18.9	42.0	>30
Duration						
Mean in seconds*	96	59	32	37	15	20
% ≤ 30 s	31.8	52.6	61.4	76.9	72.7	74.0
% > 120 s	18.8	9.6	7.7	4.2	5.8	4.6
Landing location						
Chaser return to within 0.4 ha of origin—%	57.6	74.7	92.3	93.1	96.1	95.0
Chased bird landed outside an area within 0.4 ha of origin—%	54.2	64.5	82.1	57.4	84.4	90.1
Attempted rape before or after flight						
% occurrence	12.5	1.4	2.9	0.7	0.9	2.3
n*	171	1,405	206	445	299	130

* n = total number of pursuit flights observed for each species. Information concerning some characteristics was not obtained from all pursuits so percentages (means) were calculated only from the total occurrence of each characteristic.

Three-bird Flights

Most pursuit flights fell in this category where typically 3 birds were involved, a chaser and both members of the chased pair. Both paired and unaccompanied *acuta* males instigated flights by invading an area and chasing the residents. However, most flights by other species arose when a paired male chased an intruding pair from his territory or area occupied by him. Chases were initially directed toward females but in *clypeata*, *discors* and *strepera* the mate of a chased female, which invariably joined the flight, sometimes succeeded in shifting the chaser's attention away from the female by grabbing at his back and tail feathers or by flying between him and the female. Continuous vocalization by both males usually accompanied this behaviour. However, a chaser always redirected the chase toward a female if she persisted in returning to his territory. In *platyrhynchos* and *rubripes* the female's

mate frequently did not join the flight or lagged far behind. The *platyrhynchos* pursuits usually ceased whenever the female's mate flew between her and the chaser. Frequently *acuta* males did not join flights and there was a singular lack of hostility between the males when they did.

Pursuit flights began to occur shortly after ducks arrived on their breeding ground, increased in frequency as pairs dispersed and reached a peak at nest initiation or as the females began to lay. The period of peak activity was relatively short for early arriving *acuta*, *platyrhynchos* and *rubripes*, but more prolonged for the later arriving *strepera*, *discors* and *clypeata* which spent more time between arrival and nest initiation (Table 2). There was a decrease in the frequency of pursuit flights as pair bonds dissolved and site attachment waned, however, *acuta* continued to perform chases at a relatively high frequency throughout their reproductive period.

Most pursuits were relatively short

Table 2. A qualitative comparison of social behaviour of six species of *Anas* ducks. Assessments are based upon this study, McKinney (1967, 1973) and Smith (1968)

Behaviour or Characteristic	<i>A. acuta</i>	<i>A. platyrhynchos</i>	<i>A. rubripes</i>	<i>A. strepera</i>	<i>A. clypeata</i>	<i>A. discors</i>
Paired males aggressive toward other paired males near their mates	X (rare)	XX	XX	XXX	XXX	XXX
Paired males aggressive toward unpaired males near their mates	0 (absent)	X	X	XX	XX	XX
Paired males aggressive toward males attempting to rape their mates	X	XX	XX	XXX	XXX	XXX
Paired males associate with other males before break-up of pair bonds	XXX (frequent)	XX	XX	X	X	X
Timing to nest initiation after arrival on breeding grounds	X (early)	X	XX	XXX	XXX	XXX
Timing during incubation to the break-up of pair bond	1st Week	1st or 2nd Week	2nd Week	2nd Week	3rd or 4th Week	3rd Week
Proportion of time spent by males on territories until break-up of pair bond	X (small)	XXX	XXX	XXX	XXX	XXX
Size of breeding home range	XXX (large)	XX	XX	X	X	X

ending as the pair flew away and the chaser returned to his territory. However, flights often continued when females persisted in an area or when they returned after initial chases and were chased again. Long lasting *clypeata*, *discors* and *strepera* flights were all of this kind. Pursuit flights of *clypeata* and *discors* were shortest usually rising quickly to 15 m before the chaser returned to his territory (Table 1). Pursuits in *strepera* were intermediate while *platyrhynchos* and *rubripes* flights lasted somewhat longer occasionally rising 60 to 100 m. Pursuit flights in *acuta*, which were the longest, frequently rose above 175 m and typically climbed and fell to a few metres above the ground as a female twisted erratically, followed by males in a straight undulating trajectory away from the area of origin.

The mobility of paired males was restricted once females began to remain in a particular area during the days just prior to egg laying and during egg laying. Chasing males of all species except *acuta* usually returned quickly to their territories or at least to within 0.4 ha of the origin of pursuit, the area where males were usually intolerant of other pairs. There was no apparent change in this pattern until chasing ceased sometime during incubation,

the period during which males left their mates. Chasing *acuta* frequently did not return to the area within 0.4 ha of the origin; they often landed far away, especially if the chased female landed.

Chased birds consistently landed in areas other than the origin indicating success by residents in expelling intruders. This was particularly true for territorial *discors* and *clypeata*. Our results for *strepera* may have masked the same tendency since persistent pairs were usually expelled only after several series of interactions (Table 1). In *platyrhynchos* and *rubripes*, females usually left the area quickly and *A. acuta* females were only rarely seen persisting. They usually flew farthest from the origin, sometimes more than 2 km.

In *clypeata*, *discors* and *strepera* pursuit flights the female mated to the chasing male occasionally exhibited aggression. No male to male aggression was observed by *acuta* while male to male aggression was frequent in *clypeata* and *discors*. In a majority of *strepera* pursuit flights it was difficult to determine whether the female or both members of a pair were being chased while in *acuta* and *platyrhynchos* pursuits it was more often obvious that a female was being pursued. Territorial male *strepera*, *discors* and *clypeata* chased other

paired males but not unpaired males.

In *discors*, *clypeata* and *strepera*, chasers often grabbed at the back and tail feathers of a female and sometimes at those of her mate when he flew between her and the chaser. The mates of *discors*, *clypeata* and *strepera* females made obvious attempts to intervene during pursuit flights. Before and after aerial chasing, intervention by these birds was even more pronounced. Mated males rushed vigorously at a chaser or swam between him and the female. Intervention by *platyrhynchos* males was less energetic than in *discors*, *clypeata* and *strepera*. Males of *rubripes* did not intervene while on the territory of a chaser but sometimes did if all 3 birds landed together away from the territory. Males of *acuta* did not intervene except occasionally when other males attempted to rape their mates, usually after extended flights. Contrary to these results Barash (1977) reports that male *platyrhynchos* do not vigorously defend their mates.

Chasers of all species left their mates to pursue and all except *acuta* males returned quickly to their mates. Males of *platyrhynchos*, *rubripes* and particularly *discors*, *clypeata* and *strepera* returned to their territories whether their mates were there or not and without significant difference in duration.

Inciting and Repulsion postures and associated calls were observed by chased females of all species, particularly those that persisted in an area or those whose mates did not join them in flights. Generally Inciting occurred early in the breeding season to the end of the laying period and Repulsion occurred later as females were incubating.

Attempted Rape Flights

Some vigorous, long lasting pursuits involving one female chased by several males had the form of Attempted Rape Flights (Lebret 1961). These chases often started as Three-bird Flights which were joined by other males that frequently continued to chase after the original chaser(s) had left. One could only be sure of classifying the pursuit correctly by observing attempted rape before or after the flight. It was impossible to determine whether a chaser was attempting to rape a female while the birds were in flight. These pursuits, which often left the female's mate far behind, were only rarely seen in *clypeata* (<5% of

flights) *strepera* (<5%), *discors* (<5%) and *rubripes* (<5%), occasionally in *platyrhynchos* (<10%) and were most frequently observed among *acuta* (>30% of pursuit flights).

Pursuit flights involving several chasers usually occurred when a pair flew over several territories and was chased by territorial males arising from each. Until early incubation (end of first week) most males of all species except *acuta* returned to their territories without landing elsewhere. Males of *acuta*, however, frequently persisted in following chased females and almost always tried to mount them when landing after a chase.

Females of all species, unless chased for an extended period, were successful in evading their pursuers. An apparently exhausted female landing after an extended chase would be further harassed by pursuing males yet even then she often evaded them by hiding in dense vegetative cover or by diving into the water and hiding in emergent vegetation. The low frequency of attempted rapes is evident from Table 1. Apparently successful rapes where a mounted male actually appeared to achieve intromission with the female were only observed in *platyrhynchos* (once) and *acuta* (twice).

When a chased female's mate was present during an attempted rape he usually defended the female. This defence appeared most vigorous in *discors* and *clypeata*, however even *acuta* males defended their mates (Wishart & Knapton 1978). Unpaired males were only observed in attempted rape involving *discors* (Bailey *et al.* 1978).

Attempted Rape Flights of *acuta* occurred regularly throughout the entire breeding period. For the other species there was a tendency for these longer pursuit flights to occur later in the season after incubation was underway.

Pursuit flights of *acuta* and *platyrhynchos* (11.2%) involved females that may have been 'teasing' (Sowls 1955) males in an attempt to obtain a mate. These females assumed Repulsion postures and made Repulsion calls.

Male-male pursuit flights

Pursuit flights consisting of only two males were observed by *discors*, *strepera* and *clypeata*. A territorial male usually chased a persistent male originating from a con-

tiguous or nearby territory. Many long and vigorous pursuit flights involved only males which frequently grabbed at and thrust their bills at each other. Males left their mates to chase other males with the same frequency as they chased females of pairs. Dwyer (1974) has also recorded this for *strepera*. Male-male pursuits were rare in *rubripes* and *platyrhynchos* and were not seen in *acuta*.

Territorial behaviour

The pursuit flight appears to be the major aggressive behaviour pattern responsible for spacing on the breeding ground. It is an effective means of expelling intruders from already occupied areas. Although spaced, *acuta* pairs do not behave territorially as the other five species do (McKinney 1967; Smith 1968; Titman 1973; Dwyer 1974; Seymour 1974a, b; Seymour & Titman 1978; Stewart & Titman 1980). Only females are chased from *platyrhynchos* and *rubripes* territories. If a female leaves, her mate leaves also without being chased. It appears that she leads the male there in the first place. In *clypeata*, *discors* and *strepera*, males are also excluded perhaps reflecting a greater role by the male in the choice and establishment of a territory.

Observations of tendencies toward aggression and site attachment among the six species of ducks are summarized in qualitative fashion in Table 2. The same alignment of species which was developed in Table 1 is apparent. In *acuta* and the species closely aligned to it there was less hostility towards all conspecifics and males were more sociable towards other males than the species closer to *clypeata*. At the *clypeata* end of the scale males remained site-attached longer and spent more time on their 'territories' than species towards *platyrhynchos*. The discrete territory occupied by pairs of *discors* averaged 0.69 ha near Minnedosa, Manitoba (Stewart & Titman 1980) while the overlapping territories of *platyrhynchos* pairs averaged 16 ha in the same habitat (Titman 1973).

Based upon the strength of site attachment and defensive tactics described above it must be concluded that *clypeata* and *discors* are strongly territorial and *strepera* towards *platyrhynchos* are less so. The strongly territorial species rely less upon pursuit flights for territory defence using different threat behaviours and overt rushes (Seymour 1974A; Stewart and Tit-

man 1980) The *strepera* appears to rely almost equally upon pursuit flights and other forms of aggression.

Another aspect apparent from the information presented in Table 2 and above is that the length and strength of attachment to a mate is greater in *clypeata* and *discors* than it is among the species toward *acuta*.

McKinney (1965) has associated raping with a weak pair bond. Following *acuta* pursuit flights the frequency of attempted rape was high while for the other five species it was observed relatively infrequently. Considering that *discors* and *clypeata* performed other aggressive behaviours more frequently than pursuit flights, the frequencies of attempted rape given (Table 1) are inflated estimates of their actual occurrence. Furthermore, successful rapes involving actual intromission were only observed in *acuta* and in *platyrhynchos*. In *acuta* attempted rapes occurred throughout the breeding season while in the other species they were most often observed after they laying period when females were likely attempting to reneest.

Pursuit flights undoubtedly have similar meaning for the six species considered here as evidenced by observations of interspecific involvement (Table 3). However, when different species were involved in a pursuit flight, the pursuit was most frequently abandoned within seconds of initiation. Most of these interspecific pursuits originated in flight either as a chaser rose to meet a pair flying over or joined another pursuit flight already in progress. They appeared to be mistaken reactions to intruding birds.

Discussion

The varying characteristics of pursuit flights are tied inextricably to other aspects of the social system and overall breeding strategy for each species and are thus more easily discussed together. McKinney (1973, 1975) has contrasted and compared the breeding strategies of *acuta* and *clypeata*. He has further associated Green-winged Teal *A. crecca carolinensis* very closely with the breeding strategy employed by *acuta* (McKinney 1975). From this study it appears that *discors* has a strategy very similar to *clypeata* and that the other three species considered fit between this and the *acuta* extreme.

The *clypeata* are attached to a physical site during the breeding season, defend it

Table 3. Observations of interspecific involvement in pursuit flights

Chaser	Species		Number of observations	
	Chased bird	Actually chasing	Joining a pursuit flight in progress	
<i>A. acuta</i>	<i>americana</i>	1*	1	
	<i>clypeata</i>	1		
	<i>platyrhynchos</i>	2	2	
	<i>rubripes</i>		1	
<i>A. americana</i>	<i>discors</i>	1		
	<i>platyrhynchos</i>	4	1	
	<i>strepera</i>	1	2	
<i>A. clypeata</i>	<i>acuta</i>	1		
	<i>americana</i>	1		
	<i>discors</i>	2		
	<i>platyrhynchos</i>	1		
<i>A. discors</i>	<i>strepera</i>		2	
<i>A. platyrhynchos</i>	<i>acuta</i>	1		
	<i>americana</i>	4*		
	<i>discors</i>	2	1	
	<i>strepera</i>	9		
<i>A. strepera</i>	<i>americana</i>	3		
	<i>platyrhynchos</i>	2	2	
Totals		36	12	

* 1 pursuit appeared to be in response to 'Repulsion-Teasing' by the pursued female. 1 *discors* also chased a Lesser Scaup *Aythya affinis*.

actively and form strong, long lasting pair bonds (McKinney 1967, 1973; Seymour 1974a, b). This is reflected in the short vigorous pursuit flights which terminate as a chaser returns quickly to his territory regardless of whether his mate is there or not. The stimulus to chase is simply a territorial transgression, whether by a female, a male or a pair. Males remain with females past mid-incubation and defend their territories until then. They use permanent water in deep ditches, ponds or dugouts providing a relatively dependable resource base. Individual males invest time and energy heavily in one female on their chosen territory (Seymour 1974a, b; Afton 1979).

In contrast, *acuta* males chase females, never males, for extended periods, may not return to the females they were with previously and frequently attempt to rape the chased female. They are wide-ranging and not attached to discrete local areas (Derrickson 1978). They are associated with ephemeral water areas, temporarily abundant food and an unpredictable resource base (Krapu 1974). A well developed rape strategy, a relatively weak pair bond and lack of territorial behaviour set *A. acuta* apart from the other species.

The behaviour of *discors* is very similar to that of *clypeata*. In *strepera*, there is significantly less male to male aggression and pair bonds appear to break up earlier but otherwise their pursuit flights and territorial behaviours are very similar. Table 1 reveals that the pursuit flights of *strepera* and *rubripes* are very similar, however, the latter's breeding strategy appears to most closely resemble that of *platyrhynchos*. The resource base upon which these species depend is perhaps less predictable than that of *A. clypeata* and these ducks appear more adaptable or at least they exhibit greater variability in habitat and food utilization. Male *platyrhynchos* and *rubripes* are less attentive to their mates, more wide ranging and exhibit still less male to male aggression. They still remain short of the extreme represented by *acuta* and *crecca carolinensis* (McKinney 1975).

It has been debated whether pursuit flights are sexually or aggressively motivated (Geyr 1929; Dzubin 1957; Lebreton 1961; McKinney 1965; and others). The high frequency of attempted rape following *acuta* pursuits indicates that there is sexual motivation involved while the low frequency of rape, combined with high frequencies of male to male involvement, signals

aggressive motivation in *clypeata* and *discors*. It is more difficult to deduce possible motivation in species intermediate in the suggested alignment. In these, attempted rape occurs relatively infrequently, it is unlikely that many are successful and there is little male to male aggression.

Regardless of the motivation of the chaser, pursuit flights must ultimately be viewed according to their potential benefit to the reproductive fitness of the chaser. Successful rape will quickly fertilize a female attempting to renege and this would increase the fitness of the individuals performing this activity. This likely occurs in all the species examined here but in *acuta*, which are observed in attempted rapes throughout the breeding season, it appears that individuals actually employ a raping strategy (McKinney 1973, 1975). An interesting debate involving fitness and energetics—costs and benefits—surrounds the question of when should an individual male defend one female for a long period and conversely, when should a male quickly leave a female following copulation or even rape to seek another for the same purpose. This latter tactic may be unsuccessful if a male's presence with a female enhances her chances of successful reproduction. However, raping should be to his advantage in producing a larger number of progeny at little cost in energy if his presence has little or no effect. Individual males of *platyrhynchos* through *clypeata* stay with one female at least until early incubation. This would imply that there is positive benefit to the association between male and female at this time. Factors such as habitat, food and other resources available, and population density may tip the balance in favour of one strategy over the other where otherwise the optimum may be a compromise between the two.

Recently several authors (Siegfried 1965; McKinney 1973; Dwyer 1974) have suggested that positive benefit is derived from the aggressive defence of an area by a male to provide undisturbed feeding time for his mate. For the six species in this study in most situations food itself does not appear to be limiting, thus there would

appear to be little advantage to defending the resource itself. However, a female may be prevented from spending sufficient time feeding to obtain the energy she needs during the very demanding breeding period by interacting with conspecifics.

Before eggs are laid isolation may be important in ensuring uninterrupted copulation (Hochbaum 1944). The spacing resulting from chasing and territorial behaviour serves to separate nest sites and may function to reduce predation (McKinney 1965). Several advantages accrue to those individuals behaving territorially. It is unlikely that this behaviour evolved as a result of one factor, but that it serves several different functions especially when different species are considered.

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Summary

The pursuit flights of six species of surface feeding ducks were compared. These aerial chases can be classified as Three-bird Flights or Attempted Rape Flights. Pursuit flights result in dispersion of the six species considered. Although there are important similarities in form and function, the characteristics of pursuit flights, the participants involved, raping tendencies and territorial behaviour differ considerably from one species to another. Based upon these criteria an alignment of the six species appears possible; from the strongly territorial Blue-winged Teal *Anas discors* and Shoveler *A. clypeata* through Gadwall *A. strepera* to Black Duck *A. rubripes* and Mallard *A. platyrhynchos*, with Pintail *A. acuta* exhibiting weak site attachment and a raping strategy at the opposite extreme.

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