Interspecific territoriality and competitive interactions between American Black Ducks *Anas rubripes* and Mallard *A. platyrhynchos*

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Interactions between pairs of American Black Ducks and Mallards were studied at six sites in northeastern Nova Scotia during territory establishment. Interspecific territoriality was well developed and most frequently resulted in competitive superiority by resident pairs, regardless of species. Also, intruding pairs sometimes remained on territories already occupied by the other species. Exclusion of Black Duck pairs by Mallards occurred twice.

Introduction

Pursuit flights, in which a male chases a female other than his mate, have been recorded in most species of the genus Anas, and are known in Mallards A. platyrhynchos and American Black Ducks A. rubripes (Titman & Seymour 1981). Pursuit flights are effective in expelling intruders from occupied sites and probably cause dispersal and spacing of breeding pairs of ducks (McKinney 1965). Females flee from pursuing males and these females usually do not return to the pursuit territory (Titman & Seymour 1981).

Although direct evidence was not provided, Ankney et al. (1987) suggested that competitive exclusion of Black Ducks (hereafter BD) by Mallards (hereafter M) may occur, and may be a factor in the decline of BD populations in parts of their range. Good evidence for this would be that intruding Ms usurp territories from resident BD but not vice versa.

Methods

The general study area was a 25x30 km watershed in Antigonish County in northeastern Nova Scotia. Three rivers and their tributaries flow through forest and agricultural land and drain the watershed into a tidal marsh which opens into the outer St. Lawrence River estuary. Six dispersed wetland sites, the water surfaces of which ranged in size 0.5-3.0 ha, were the focus of observations because they were the only sites occupied by both species. These sites in agricultural habitat were among the most nutritionally-rich wetlands in the watershed (Seymour in prep.).

Each site was accessible by road and most observations were from vehicles; some were made from portable blinds. Data were collected when males were attempting to establish territories. M and heterospecific pairs (always male BDs x female Ms) were intensively observed for as long as possible whenever they were located. I recorded all behaviour observed during interactions. Ms could usually be identified as individuals because there were so few (0-2 pairs and 0-3 males each year) other Ms on the study area, and because some males could be identified by unique morphological features. Male BDs, and some Ms, were marked with nasal discs (Bartonek & Dane 1964) or with patagial tags (Anderson 1963). Some males were captured during the period of observation in traps made of poultry wire and baited with a live female or grain. However, many BD, and some M, remain on my study area throughout the annual cycle. I use bait traps to capture birds during the

winter, and I also capture and mark ducklings. Consequently, there are marked birds on my study area prior to the beginning of territory establishment. Hybrids were rare and only birds that had the morphological appearance of "pure" M or BD were included in the study.

Pursuit flights, chasing across the water and threatening by males were recorded as hostility. M males in this study area force copulate with BD females (Seymour 1990), but herein I have included only those interactions in which hostility was observed. In each interspecific encounter reported in Tables 1 and 2, I observed chasing across the water, grabbing at and pulling feathers, or pursuit flights directed toward the intruders by the resident male. Hostility by intruders toward incumbents at a site, and persistence there for more than one day, were considered an attempt by intruders to remain at that site. Intruders that left a site during pursuit flights were considered displaced if they did not return on that occasion, but I did not consider an intruding pair to be permanently displaced until there was no evidence of them for several days at the water surface of the contested site.

Results

BD and M intraspecific territorial behaviour is well developed in this study area, and pursuit flights are the most obvious manifestation of territoriality (Seymour & Titman 1978). In this study, both BD and M residents maintained exclusive territories against conspecifics. Infrequency of pursuits and the short time that intruders remained near territories indicate that conspecific intruders were not persistent (Table 1).

Hostility associated with territory defense was well developed between BD and M (Table 2). One or all of these hostile behaviours may have occurred during an interaction between pairs, and persistent chasing over the water usually resulted in pursuit flights. However, males were significantly (X^2 = 16.422, df = 1, P<.001) less successful defending territories against interspecific intruders than they were against conspecific intruders (Table 1). Interspecific hostility at a site ultimately resulted in three possible outcomes. The most frequent outcome was competitive superiority by the resident, regardless of species. Assuming that there would be no difference in ability of residents versus intruders to dominate at a site, residents were significantly (X^2 = 6.818, df = 1, P>.01) more successful (24 residents *v* nine intruding pairs) in defending territories than were intruders in either sharing the site or displacing incumbents. Consequently, intruding BD and M pairs usually left territories when pursued by interspecific occupants. On 18 occasions, pairs that occupied adjacent sites were chased when

Table 1. Outcome of conspecific and interspecific territorial interactions involving identifiable Black Duck (BD) and Mallard (M) pairs at six contested sites, 1972-90.

Resident pair		Intruding pair[a]		Hours	Pursuit flights[b]			Days remained[c]			Outcome[d]		
Species	*n*	Species	*n*	Observed	*n*	Mean	Range	*n*	Mean	Range	Departed	Shared	Displaced
BD	33	BD	46	512	109	2.4	1-3	59	1.3	1-2	46	0	0
M	8	M	8	164	13	1.6	1-2	10	1.3	1-2	8	0	0
M	10	BD	14	210	61	4.4	1-6	47	3.4	1-6	10	4	0
BD	19	M	19	409	91	4.8	3-7	89	4.7	1-6	14	3	2

[a] Different intruding pairs.
[b] Mean pursuit flights per intruding pair.
[c] Mean days intruders remained on sites before departing .
[d] Intruding pairs departed from, or shared contested sites, or they displaced the incumbents from sites.

Table 2. Territorial hostility by Black Duck (BD) and Mallard (M) males directed toward interspecific intruders.

Resident Species	male [b]*n*	Intruding Species	pair [c]*n*	[a]Encounters	Threat	Chase over water	Pursuit flight
BD	19	M	19	213	148	49	91
M	10	BD	14	129	47	64	61

[a] Occasions when a male demonstrated some form of hostility toward an intruding individual or pair.
[b] Total different territorial males involved in interactions.
[c] Total different intruding pairs involved in interactions.

they intruded on their neighbour's territory. On eight of these occasions, BD males of pairs that were chased from a M territory, later chased the M pair when they intruded on the BD territory.

Intruding BD pairs sometimes remained on territories already occupied by M, and vice versa, despite pursuit flights and other hostility being directed toward intruders by incumbents. Table 1 shows that BDs and Ms were more persistent at sites occupied by the other species, than at sites occupied by conspecifics. On four occasions, BD pairs successfully shared contested sites that were previously occupied by a M pair. Similarly, eventual sharing of contested sites occurred on three occasions when intruding Ms remained on territories occupied by BDs. Four BD pairs, which had earlier been repelled by resident M males, established territories at the contested sites within three days after desertion by the resident Ms. Two of these BD pairs had occupied the contested sites the previous year. When two pairs persisted at the same site, the highest frequency of hostility between them, particularly pursuit flights, occurred during the day of their first encounter. On the seven occasions when BD and M pairs occupied the same site throughout the breeding season (Table 1), hostility was infrequent after three or four days, and thereafter the two males usually sat together when their mates were away. These males sometimes threatened or occasionally rushed at the other when the aggressor's mate re-joined him on the territory.

Probable competitive exclusion occurred on two of the occasions when Ms persisted at territories occupied by BDs (Table 1). In each case, the BD males had defended their territories against conspecifics for 5-6 days before encountering the Ms. Hostility, including pursuit flights, occurred between the BD and M pairs for three days before the BDs left these sites and nested elsewhere in the watershed. Desertion by the BDs was not a consequence of losing clutches of eggs, which results in desertion of territories in this population (Seymour & Titman 1978).

Discussion

Most frequently, interspecific territorial interactions resulted in competitive superiority by residents, regardless of species. However, sometimes BDs and Ms remained at sites already occupied by the other species and shared these sites with incumbents. There were two cases of apparent competitive exclusion in which M pairs usurped BD territories.

Presence of M pairs at six sites in this study area could reduce the reproductive fitness of BD females, which are philopatric in this population (Seymour 1991). Each breeding season since 1972, there has been perennial intraspecific competition for these sites by BDs, and they are maintained as exclusive territories (Seymour in prep.). Furthermore, these are widely dispersed sites where females and broods forage. Presumably, exclusion of BD by Ms, or even sharing of the site, could diminish the reproductive potential of a female BD.

Sharing sites with Ms may be detrimental to female BD in two ways. Hostility by M males can disrupt foraging and other activities such as copulation (Seymour 1990). But perhaps more importantly, forced copulation, a well developed secondary mating strategy in male Ms (McKinney 1985), is directed toward female BDs by male Ms on this study area (Seymour 1990). Persistent hostility, and/or sexually motivated behaviour directed toward female BDs, may diminish the willingness of BD females to persist at sites occupied by Ms. This would reduce competitiveness of BD pairs for these sites and would support Ankney *et al.* (1987) who speculate that competitive exclusion can be a factor in the concomitant increase in Ms and decrease in BDs in parts of their range. Indeed, when quality and/or availability of suitable breeding sites is a factor in determining reproductive success, competitive superiority of a pair of Ms at a site may diminish the fitness of a BD female during that breeding season. Competitive superiority may be as important as competitive exclusion in the expansion of M into BD range.

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