Aggression and behavioural dominance in wintering Mallard *Anas platyrhynchos* and American Black Duck *A. rubripes*

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Abstract

Environmental change can reduce species barriers and increase interactions between closely-related species. Furthermore, for sister taxa that have little niche differentiation, behavioural dominance can affect the distribution and abundance of the subordinate species. Here, aggression and behavioural dominance were investigated between two closely related sister taxa, the Mallard *Anas platyrhynchos* and American Black Duck *A. rubripes* (hereon Black Duck) at Cayuga Lake, New York, from January–March in 2015–2017. Specifically, the observed number of aggressors, aggressive behaviours performed, aggressive behaviours received and the number of victims of aggression, determined by analysing video footage obtained from Go-Pro cameras mounted in traps baited with corn, were compared to expected frequency of these activities. Expected frequencies were based on the number of individuals of each species and sex identified in the footage at a trap site during each recording period. Behavioural dominance also was determined by quantifying the probability of a species-sex class being deterred from using these feeding sites when threatened. Male Mallards were more common, aggressive and dominant than Black Ducks. Female Black Ducks were deterred from feeding sites by aggression from male Mallards more than other species-sex classes. Results suggest that Mallard dominance could decrease the carrying capacity for Black Ducks at our wintering area study site, through interference during foraging and displacement from feeding locations. If this

pattern is occurring elsewhere, it could contribute to changes in distributions, and possibly declines in abundance, of Black Ducks through secondary contact with Mallards.

Aggression and behavioural dominance can lead to competitive exclusion and may regulate populations and spatial distributions of animals (Lack 1968; Schoener 1974; Gauthreaux 1978; Nudds 1983). Dominance can be especially important when resources are limiting or weather conditions increase thermoregulatory costs (Appleby 1980; Brodsky & Weatherhead 1985; Hannon *et al.* 1987). Dominant individuals may monopolise food resources, leading to longer residency time at feeding sites, which can lead to greater survival and reproductive success (Fretwell 1969; Schneider 1984; Hepp 1986; Alexander 1987). In stable environments, resource partitioning between closely related species is often well-developed, whereas in recently altered habitats where resources have changed, competition may be enhanced (Mayr 1970; Lack 1971). These changes can facilitate niche overlap and aggression, and behavioural dominance may eliminate subordinate individuals from certain habitats or cause reductions in their spatial distribution and abundance (Elton 1958; Lack 1971; Mooney & Hobbs 2000).

The American Black Duck *Anas rubripes* population, which decreased in numbers by *c.* 50% between the 1950s and 1990s, has since stabilised but not recovered to historic levels despite increased conservation measures (USFWS 2018; see also Coluccy *et al.* 2020, this volume). A diversity of hypotheses exist for the decline in Black Duck abundance, including loss and modification of breeding and wintering habitat, overharvest from hunting, and competitive exclusion by Mallard *A. rubripes* (Goodwin 1956; Ankney *et al.* 1987; Longcore *et al.* 1998; Mank *et al.* 2004; Maisonneuve *et al.* 2006). Once largely allopatric, Mallards have expanded into Black Duck breeding and wintering areas, facilitated by human-caused habitat change and release of captive Mallard for recreational harvest in the Black Duck range (Heusmann 1974; USFWS 2013a; Lavretsky *et al.* 2019a). The convergence of wintering areas for these species has resulted in an increased potential for competition for space and food resources (Hoysak & Ankney 1996) and behavioural dominance by Mallard over Black Duck could exacerbate the Black Duck's population decline (Petrie *et al.* 2012).

Mallard and Black Duck are among the most closely-related duck species, hybridise regularly, and have little ecological separation (Hepp & Hair 1984; Brodsky & Weatherhead 1985; Hoysak & Ankney 1996; Lavretsky *et al.* 2019a, b). These factors could contribute to aggression between these species, especially between males, because females are attracted to the most dominant males, even if they are not of

the same species (Brodsky *et al.* 1988). Dominant individuals at wintering areas would have access to high-quality, energy-dense food, and have more efficient nutrient storage for winter survival (Hoysak & Ankney 1996). Moreover, events of one season can affect survival and reproduction in subsequent seasons (Sedinger *et al.* 2011) (*i.e.* carry-over effects), with survival, formation of a strong pair bond during winter and acquisition of nutrient reserves for migration being precursors to successful reproduction in waterfowl. Dominance therefore may allow for greater reproduction *via* carry-over effects (Hepp 1984; Sedinger & Alisauskas 2014; Sedinger *et al.* 2011). For example, in ducks, weather influences the timing of migration (Schummer *et al.* 2010), but a threshold of lipid reserves is also necessary to cause migratory restlessness (Newton 2006). These lipid reserves are used not only to fuel migration to the breeding areas but, in both Mallard and Black Duck, as endogenous energy reserves required (with protein and other nutrients) for egg production (Sedinger & Flint 1991; Baldassarre & Bolen 2006; Stafford *et al.* 2014). A subordinate species or sex excluded from prime feeding sites, and subject to greater intra- and interspecific competition and aggression during winter, therefore may have reduced ability to gain energy and nutrient reserves on the wintering grounds, required for successful reproduction during the breeding season (Hepp 1984; Hepp and Hair 1984; Sedinger & Alisauskas 2014).

This study determined patterns of aggression to see whether behavioural dominance occurs among species-sex classes of sympatric wintering Mallard and Black Duck in the wild. Earlier research used trials with captive ducks (*e.g.* Brodsky *et al.* 1988; Hoysak & Ankney 1996) or did not include Mallard (*e.g.* Hepp & Hair 1984). We therefore observed aggressive interactions between ducks at an energy-dense feeding site, in a northern wintering area for both species in eastern North America, to investigate the outcome of interactions between the species-sex classes. The prediction, based on prior trials with captive ducks (Brodsky *et al.* 1988; Hoysak & Ankney 1996), was that Mallard would be more aggressive than Black Duck. Moreover, we predicted that males of either species would be more dominant than the females, because these ducks are paired during winter, males outnumber females, and males are known to defend pair bonds from advances by unpaired males (Hepp & Hair 1984; Hoysak & Ankney 1996).

Methods

The study took place at Cayuga Lake, within the Finger Lakes region of central New York (42°41.5'N, 76°41.3'W) in the middle of the North American Atlantic Flyway (Effler & Peng 2014; USFWS 2013b). Cayuga Lake is bordered to the north by a diversity of shallow wetlands and rivers owned by the United States Fish and Wildlife Service (USFWS) Montezuma National Wildlife Refuge, the New York State Department of Environmental Conservation (NYSDEC), Northern Montezuma Wildlife Management Area, private hunt clubs and private agricultural land (Ryan 1972; USFWS 2013b). Thousands of ducks, geese and swans use Cayuga Lake's consistently open water during

winter (Ryan 1972; Ostrander 2016). Average (± s.e.) annual duck-use-days (*i.e.* number of ducks × days of residency) in the region has been estimated as ≥ 610,870 ± 82,806 duck-use-days for Mallard and ≥ 135,790 ± 24,198 for Black Duck during January–March in 2000–2017 (Ostrander 2016).

Behavioural interactions between Mallard and Black Ducks were studied by observing birds around baited, walk-in traps during January–March in 2015–2017 (State University of New York College of Environmental Science and Forestry Institutional Animal Care and Use Committee Protocol #150601). Traps were set by New York Department of Environmental Conservation and USFWS staff as part of normal winter banding operations. Traps were baited with corn, an energy-dense food and an ideal lipid source for waterfowl throughout the winter (Baldasssarre & Bolen 2006). Most adjacent shallow wetlands were frozen during winter and snow cover typically precluded foraging on waste grain in nearby agricultural fields. These baited sites therefore likely provided the greatest density of high-energy food resources for ducks on Cayuga Lake during winter, and were the most logistically practical areas for monitoring aggression and behavioural dominance, with aggression and behavioural dominance readily detectable if it existed among species-sex classes. Traps were placed ≤ 3 m from the water and corn was used as bait inside traps and outside ≤ 0.5 m from the entrance.

Remote cameras were used to gather data on bird interactions at traps. Go-Pro Hero 4 cameras were placed in the centre of the back panel of open, baited traps, facing the funnel entrance, 3 times per week. Each morning, the cameras were placed to cover the greatest possible viewing area in front of the funnel entrance and video recordings taken from sunrise until the camera battery expired. Dummy cameras – painted blocks of wood of similar colour and shape as the Go-Pro cameras – were placed in traps without Go-Pro cameras to reduce bias associated with camera placement. Go-Pro cameras were rotated systematically among trap locations (*n* = 6 locations, > 3 km apart) between successive trap mornings throughout the trapping period.

The videos were watched to quantify bird abundance and agonistic interactions between each species-sex pairing. Footage of ducks outside the traps was observed and behaviours were recorded by species-sex class, noting: 1) abundance of ducks outside of traps, 2) number of individuals instigating aggressive behaviours, 3) number of aggressive behaviours being performed, 4) number of aggressive behaviours received, and 5) number of individuals receiving aggressive behaviours (*i.e.* victims). Plumage and bill colour were used to determine species and sex (Baldassarre & Bolen 2006). When the sex of a Black Duck could not be determined (4.2% of all ducks), that individual was omitted from the analysis. Aggressive behaviours included jabbing with the bill, biting, chasing, threatening posture and attack with open-bill or head pumping threat-displays (Paulus 1983). When an aggressive behaviour was performed at the entrance to the trap, the species-sex classes of the aggressor and victim, and whether the victim was deterred from using the baited feeding area within the trap were

recorded. A duck was considered to have been deterred from feeding if the victim went off-screen or retreated back to the water without returning to the trap. If an aggressive behaviour occurred where bait was available outside the trap, but the victim continued to feed or entered the trap, it was counted as remaining at the feeding site. During observations, ducks could have moved out of camera shot and returned to the video frame, but the wide-angle setting was used to maximise ability to follow individual birds, and it was assumed this potential error was similar among species-sex classes.

A G-test of goodness of fit was applied to determine if data could be pooled among recording periods. Data were heterogeneous among observations and within years and sites ($G_{72} \geq 241.5$, $P < 0.001$), so a Chi-square Goodness-of-fit test with a Bonferonni Correction was used for individual recording periods (*i.e.* α = 0.0018). The percentage of the number of aggressors, number of victims, number of aggressive behaviours initiated and number of aggressive behaviours received by each species-sex class was defined as the observed population. Percentages of ducks from each species-sex class recorded outside the traps were treated as the expected population in determining whether observed frequencies of behavioural interactions differed from expected values. For example, if 25% of ducks observed outside of a trap were male Mallard it would be expected that 25% of aggressive behaviours would come from the male Mallard category. Ducks typically arrived and left the feeding site as a single flock, resulting in the abundance

of ducks for each species-sex class being consistent throughout the morning recording period at the trap. As such, we used the maximum number of individuals by species-sex classes outside the trap as the expected frequencies of behaviours. When a significant difference was detected between the observed and expected frequencies, the percentage of recording periods during which behaviours occurred more or less frequently than expected were calculated for each species-sex class. For each species-sex class of the aggressor, logistic regression was applied to determine if the probability of deterrence of victims differed among species-sex classes, with year included as a covariate, and a Tukey's Honest Significant test was applied to determine differences among species-sex classes at α = 0.05. Mean values are given ± s.e. throughout.

Results

Observers watched 9,861 minutes of video from 95 separate recording periods, made during January–March in 2015−2017. Ducks were present for 72 of these recording periods (mean = 105 ± 5 min; median = 102 min; range = 22–262 min) and we observed a total of 3,452 agonistic interactions (mean = 43 ± 7 occurrences per video session; median = 21; range = 0–279). The percentage of male Mallard was greatest among species-sex classes (54.6 ± 2.8% of individuals), followed by female Mallard (31.7 ± 2.1%), male Black Ducks (8.0 ± 1.9%) and female Black Ducks (5.7 ± 1.5%).

Number of aggressors

The number of aggressive individuals differed from the expected number during

four of 72 observation periods (5.6%; Supporting Materials, Table S1a). Male Mallard and female ducks were more and less aggressive than expected 100% of the time (n = 4), respectively; male Black Ducks were more aggressive than expected 75% of the time (n = 3).

Number of aggressive behaviours

The number of aggressive behaviours differed from the expected number during 53% of recording periods (n = 38; Supporting Materials, Table S1b), with male Mallard more aggressive than expected (68.4% of periods) and male Black Duck (60.0%) and female ducks (Mallard = 63.2%, Black Duck = 93.4%) less than expected.

Number of victims

The number of victims differed from the expected number for 23.6% of recording periods (n = 16; Supporting Materials, Table S1c). Among species-sex classes, male Mallard were victims of aggression least during these recording periods (35.3%; female Mallard = 41.2%, male Black Duck = 43.7%, female Black Duck = 40.0%).

Number of aggressive behaviours received

The number of aggressive behaviours received by these victims differed from the expected number for 44.4% of recording periods (n = 32), with male Mallards receiving these behaviours less than expected during 68.8% of recording periods. The number of aggressive behaviours received by female Mallard, male Black Duck, and female Black Duck were equal or nearly equal between occurring more (female

Mallard = 43.8%, male Black Duck = 46.7%, female Black Duck = 50.0%) or less often than expected.

Probability of deterrence of victims

When a male Mallard was the aggressor, female Black Ducks had a greater probability of being deterred from feeding sites than other species-sex classes ($F_{3,1021}$ = 3.08, P = 0.03; Fig. 1). When female Mallards or male Black Ducks were the aggressor, the probability of deterrence was similar among species-sex classes ($F_{3,494}$ = 1.97, P = 0.12 and $F_{3,309}$ = 1.37, P = 0.25, respectively; Fig. 1). Female Black Ducks were the least aggressive species-sex class (n = 78 aggressive interactions), but when they were aggressive towards other female Black Ducks there was a greater probability of deterrence for female Black Ducks than for other species-sex classes ($F_{3,75}$ = 4.30, P = 0.02; Fig. 1).

Discussion

Previous studies report little spatial partitioning between Mallard and Black Duck where the two species coincide (Huesmann 1974; Maisonneuve 2006; Petrie *et al.* 2012), and Black Duck occurred at only 5% of locations where Mallard are absent from the Cayuga Lake study area (Bleau 2018). The convergence of wintering areas for these species therefore has resulted in an increased potential for competition for space and food resources (Hoysak & Ankney 1996). Analysis of video recordings of interspecific and intraspecific interactions at our study sites confirmed that all species-sex classes exhibit aggression, but male Mallard were more aggressive and received
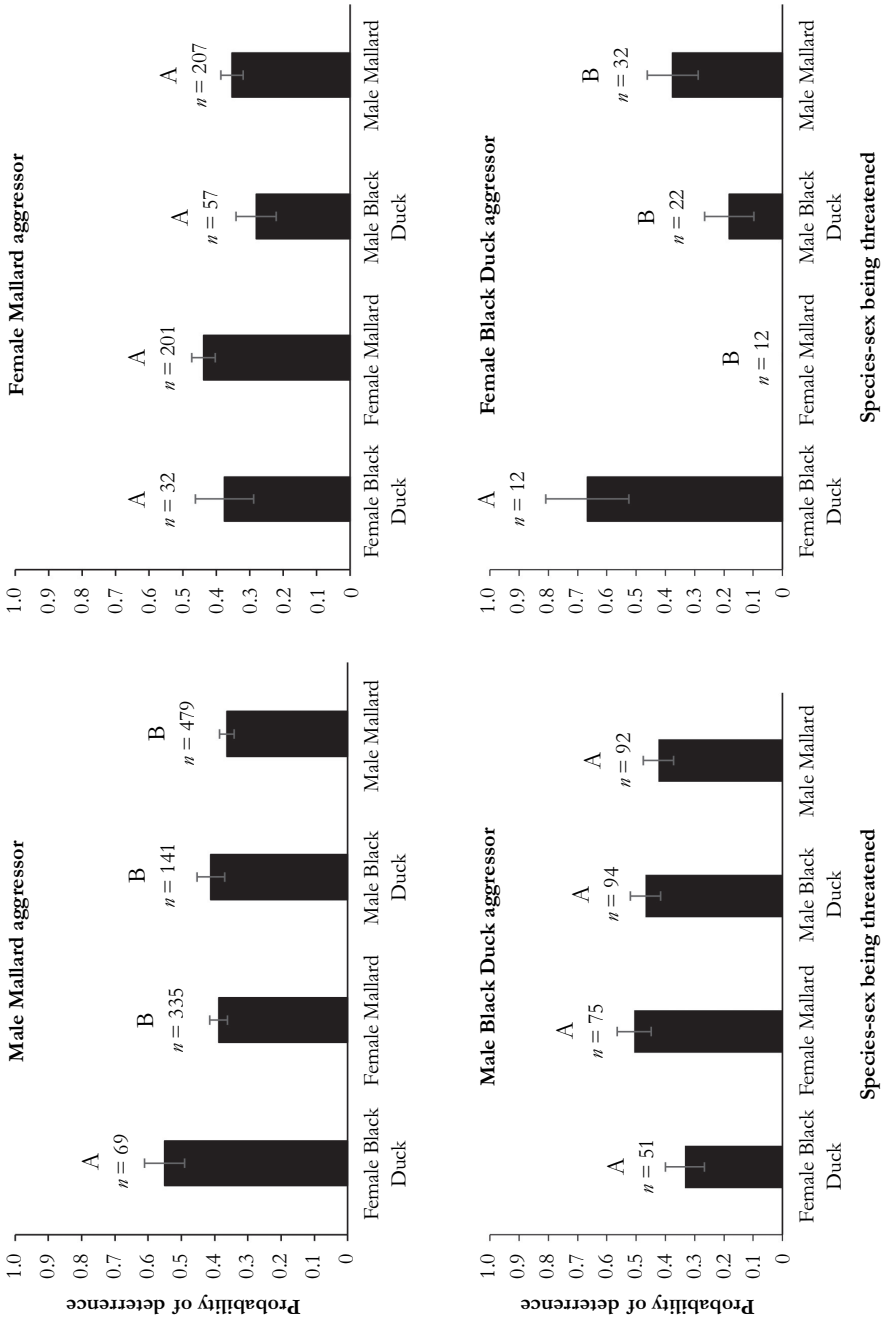
Figure 1. Probability of each species-sex class being deterred from a feeding site by aggressor species-sex classes at Cayuga Lake, New York, during January–March in 2015–2017. Within aggressors, different letters denote significant difference at α = 0.05.

fewer aggressive behaviours than expected. Further, female Black Duck had the greatest likelihood of being deterred from using feeding sites (55%) when male Mallard were the aggressor (compared to 36–41% for other species-sex classes). Proportions of Mallard and Black Duck observed at foraging sites during recording periods (Mallard = 86.3%, Black Duck = 13.7%) were relatively similar to those from winter counts of the study area (Mallard = 81.8%, Black Duck = 18.2%) (Ostrander 2016; Bleau 2018), suggesting that the study sites are representative for the two populations wintering in the Fingers Lak region.

Trap sites baited with corn represent the greatest density of high-energy food in the landscape, thereby increasing the opportunity to detect behavioural dominance. While dominance may be manifest to a lesser degree outside of the trap sites, here behavioural dominance was tested at the patch scale to infer whether Mallards may exclude Black Ducks from foraging at high-quality patches and thus interfere with their potential food intake. Overall, it was concluded that male Mallard were dominant at the trap sites on Cayuga Lake. Given that Mallard were ubiquitous in the study area, it is possible that the Black Ducks were unable to avoid Mallards not only at these but at other suitable feeding sites. Such a scenario could reduce the carrying capacity for wintering Black Ducks in our study area, because their food intake at energy-dense sites could be reduced through interference or exclusion by Mallards limiting the amount of accessible foraging habitat and food resources especially for female Black Ducks (Mayr 1970).

Pair formation in Mallard and Black Duck occurs from October–February, with paired birds remaining together until summer nesting, and unpaired males are common because males outnumber females (Baldassarre 2014). In our study, male Mallards outnumbered female Mallards by 22.9%, whereas there were only 2.3% more male Black Ducks than female Black Ducks. Hence, the abundance of unpaired male Mallards could contribute to their increased aggression by contesting paired males for their females. There was no strong evidence for a difference in the number of aggressive individuals, in comparison to the expected frequency, but there was greater evidence for male Mallard dominance described through the number of aggressive behaviours given and aggressive behaviours received. This suggests that dominance may manifest to a greater degree from repeated aggressive behaviours by a few male Mallard, rather than an abundance of aggressive male Mallard, although monitoring of known individuals is required to provide confirmation. Overall male Mallards were victims of aggression much less than expected, despite that they were the most common duck on the study area and male-Mallard-to-male-Mallard aggression occurred regularly. Waterfowl aggressive behaviours can result from mate defence or the need for foraging dominance to meet energy needs (Hepp 1984). If mate defence was the primary reason for aggression then male Mallards should have been the victims of aggression more than expected. Rather, the patterns in our results suggest aggression occurred from a need to be dominant at foraging sites and not mate defence. For

individuals receiving aggression and being deterred from foraging sites, the number of aggressive behaviours by male Mallard is likely the most important factor affecting their use of the site.

Behavioural dominance on the wintering areas enables ducks to secure quality foraging opportunities and can deter subordinates (Hepp 1984). Black Ducks provided with food and water *ad libitum* have been shown to have stronger pair bonds throughout the winter period than those on restricted diets (Hepp 1986). Thereafter, the paired ducks tended to be dominant and secured foraging sites to a greater degree than subordinate, unpaired individuals (Hepp 1986). Black Duck deterrence from foraging by Mallards could thus have consequences for pairing and remaining paired, which is a crucial precursor to successful reproduction. Spatial overlap and competition with Mallards also could result in Black Ducks selecting sites of lesser forage quality, again affecting their energy and nutrient reserves in preparation for the breeding season. Consistent with Black Ducks using sites of lesser forage quality, Mallards have been shown to have greater fat reserves than Black Ducks where they are sympatric during winter (Hanson *et al.* 1990). On this study area, Black Ducks occurred where Mallard were absent only 5% of the time, and these were not at the energy-dense trapping locations (Bleau 2018). We expect that the feeding areas where Black Ducks occurred alone had a lower density of food (*i.e.* were of poorer foraging quality) than the energy-dense trapping sites, but further assessment of food resources at sites with and without Mallards, as well as

measurements of body condition, would help to clarify the effects on Black Ducks of the behavioural dominance by Mallards detected in this study.

These results suggest that behavioural dominance could play some role in the consistent replacement of Black Ducks by Mallards from west to east throughout North America over the past 100 years. Black Ducks excluded from prime feeding areas could fail to acquire sufficient lipid stores after winter, experience a longer period of hyperphagia in spring, delay migration, and arrive on the breeding grounds after Mallards have already established breeding territories (Devries *et al.* 2008; Petrie *et al.* 2012). Early arrival in the breeding range influences establishment of territories on the most productive wetlands, increases nest success, increases the likelihood of re-nesting and, on average, results in greater likelihood of reproductive success (Baldassarre & Bolen 2006; Devries *et al.* 2008). Waterfowl are highly philopatric to breeding, staging and wintering areas (Baldassarre & Bolen 2006). Black Duck declines, at least partially, may result from the behavioural dominance of Mallard during the non-breeding period when energy resources are acquired for survival, as fuel for migration, and as endogenous nutrient resources for egg formation on breeding. Along with the tendency for Mallard and Black Duck to use the same ecological niches, results described here for the two species foraging at the patch scale suggest that range collapse of Black Ducks through secondary contact with Mallards is a plausible contribution to Black Duck decline. Lastly, given the continued transfer

of genes from birds reared on game farms into the North American Mallard population (Lavretsky *et al*. 2019a, 2020), it will be important to understand if there are differences in dominance between wild and game farm Mallards, because it could have implications for Black Duck conservation.

Acknowledgements

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Photograph: Montezuma Confusion Trap, full of Mallards, by Frank Morlock/NYSDEC.