ARTICLE CASE

The American Black Duck: Three Decades of Science-Based Adaptive Management

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ABSTRACT The American black duck (*Anas rubripes*) population declined by 50% between 1955 and 1985, prompting more than three decades of intensive scientific research and strategic management. Analyses of band recovery data suggest that the historical declines may have been caused in part by harvest, but even with restrictive hunting regulations implemented in the mid 1980s, populations have not recovered. Increasing competition and hybridization with mallards (*Anas platyrhynchos*), coupled with habitat loss and fragmentation on northern breeding grounds are hypothesized to have contributed to a lower continental black duck population. Simultaneously, there is a concern that declines in the quantity and quality of wintering habitat—coastal salt marshes of the eastern United States—may have deleterious cross-seasonal effects on black duck demographics. Black ducks have a long legacy of intensive research and management, and ongoing threats to their populations make this a well-rooted and timely case study in science-based conservation.

KEY MESSAGE

1. Learn about potential causes underlying the historical decline of the American black duck, an icon of east coast salt marshes in the United States
2. Understand how researchers prioritize and investigate the behavioral and ecological processes that drive population abundance
3. Use field data to build a scaled-down model of ecological carrying capacity (Supplementary Materials), identical to the process used by managers to set conservation and research priorities

INTRODUCTION

The American black duck (*Anas rubripes*) is a monochromatic duck that is part of the mallard (*Anas platyrhynchos*) species complex, which currently breeds primarily in the boreal forest of eastern Canada and spends the winter in the salt marshes along the Atlantic coast of the United States [1]. American black ducks are sought after by hunters because they are considered more wary than other waterfowl and are quality table fare [2]. These ducks are prized throughout the Mississippi and Atlantic Flyways, but because they are most common in the tidal marshes of the Atlantic coast, they are a flagship species for the conservation of these particular habitats.

Black duck populations declined by 50% between 1955 and 1985, and while populations in the Atlantic Flyway have since stabilized, black ducks have never recovered to historic levels (Figure 1). In 1986, the United States and (Great Britain on behalf of) Canada signed the North American Waterfowl Management Plan [3], one effect of which was the creation of the Black Duck Joint Venture, an interagency task force charged solely with guiding the research and management of this charismatic species. Over the past 30 years, researchers have investigated the behavior and ecology of black ducks, refining our understanding of population drivers and improving conservation delivery programs. There are few animal species so well studied, and ongoing efforts to confront looming threats such as sea level rise make black duck management a well-rooted and timely case study in science-based conservation. Here, we reviewed the literature to trace the history of black duck science and conservation, noting points of contention where appropriate, and finally

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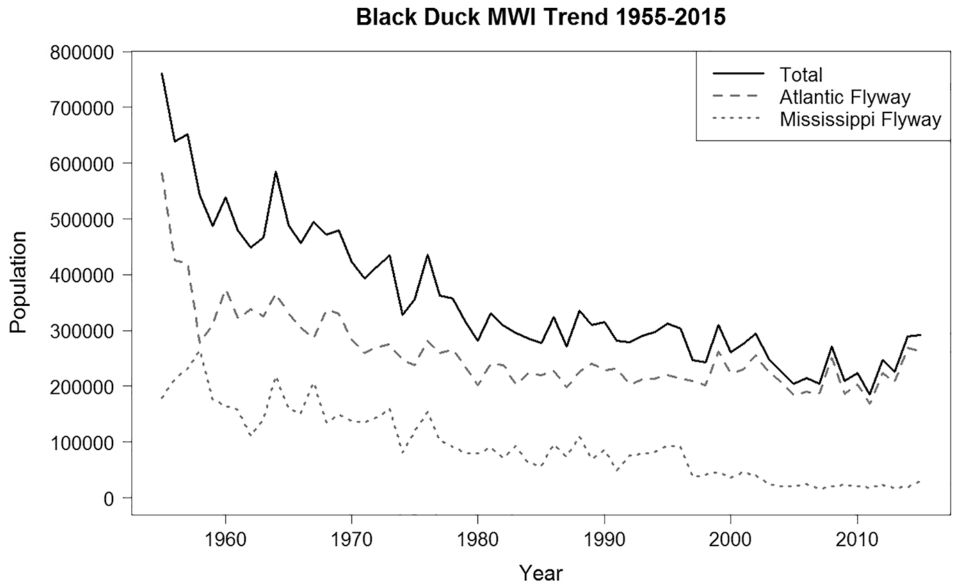

FIGURE 1. Mid-winter Waterfowl Survey (MWS) trends for American Black Ducks (*Anas rubripes*) in the Atlantic and Mississippi Flyways, 1955–2015.

ending with the current state of the art in applying well-parameterized ecological models to waterfowl conservation. Our goal in structuring the paper this way is to highlight the process of developing a science-based management program, as hypotheses are iteratively proposed, investigated, and updated. Adaptive resource management ("learning while doing") explicitly acknowledges sources of uncertainty and focuses on their reduction, with the goals of improving scientific understanding and conservation effectiveness—and black ducks make an ideal case study.

CASE EXAMINATION

By the early 1980s, the total black duck population had declined by more than 50%. The Atlantic Flyway population has since stabilized, but black ducks in the Mississippi Flyway have continued to decline (Figure 1) which suggests some important differences between these populations [4]. With a near-complete lack of information on ecological drivers of black duck population dynamics, biologists first looked to the basic tenets of wildlife management [5], where

$$\begin{aligned}\Delta \text{ Population} &= \text{Births} + \text{Immigration} \\ &\quad - \text{Deaths} - \text{Emigration}\end{aligned}$$

With consistent trends in the surveys throughout the entire range of the black duck, immigration and emigration likely were not factors driving changes in black duck populations, leaving only productivity and mortality to consider. In terms of research and management, direct morbidity and mortality were addressed forthwith. This was followed in later years by research on breeding grounds productivity (as it related to breeding habitat quality and interspecific competition) and finally to nuanced cross-seasonal demographic effects of wintering habitat quality.

Direct Morbidity and Mortality

Winter is a critical time for black ducks due to the high energetic demands of surviving winter weather in salt marshes [6, 7]. In periods of cold temperatures, black ducks exist under a negative energy balance, and therefore, they must maximize energy intake and minimize energy expenditure [6, 8]. Failure to compensate for cold temperatures with reduced movement and increased food intake can cause substantial mortality events. For example in late February–March 1960, a prolonged cold spell froze the New Jersey salt marshes and made wetland food inaccessible. The result was that body mass of black ducks declined by an average of 40% and ultimately thousands of black ducks were found dead [9, 10]. Moreover, even when weather does not directly cause mortality, declines in body condition make ducks more susceptible to hunters [11].

Of the possible factors that may influence the American black duck population, harvest is the easiest variable that can be quickly adjusted by wildlife managers (see chapter 16 in Cooch and White (2017) for a worked harvest example using black duck banding data [12]). After 30 years of precipitous declines, in 1981 the Atlantic Flyway Council called for a reduction in daily black duck limits; in fact, the Audubon Society and the Humane Society even sued the federal government to close black duck seasons entirely [13]. Bag limits were reduced from six to two birds during the 1983–1984 season and then to one bird in most states a few years later [13]. This raises an important case study question: *While such emergency stop-gap measures may have seemed prudent at the time, what science was used to validate these regulations?*

There are two competing hypotheses regarding how harvest and natural predation interact: specifically, whether mortality is additive or compensatory. Additive mortality assumes that human harvest directly adds to natural mortality, taking a relatively larger toll on duck populations. The compensatory mortality hypothesis assumes that as increasing numbers of ducks are harvested by hunters, natural mortality from predators declines in a compensatory manner [14]. The best evidence from historical band-recovery data indicates that mortality rates were likely additive during the 1950–1970s, but shifted to compensatory after restrictive regulations were put in place—suggesting that high harvest rates may have contributed to historical population declines [15, 16]. Mortality likely remains partially additive at local spatial scales [17], and so black duck harvest remains restrictive. Nevertheless, it appears that harvest was not solely responsible for suppressing black ducks, because the population never recovered to historic levels after hunting was restricted. Interacting effects seem likely: for example, habitat loss, degradation, and fragmentation may have reduced carrying capacity such that the harvestable surplus was reduced, leading to additive mortality.

Breeding Grounds Productivity

Despite implementation of increasingly restrictive harvest regulations, when black duck populations did not return to historic levels, it became clear that other factors must be driving black duck demographics, and so attention turned to the breeding grounds [18]. Temperate-nesting dabbling ducks tend toward an r-selective life history strategy, and indeed, the most rigorous data collected on mallards confirm that populations are more sensitive to perturbations in breeding grounds productivity than to adult survival [19]. Most North American waterfowl breed in dynamic prairie systems, so when wetland conditions are good, duck populations increase substantially [20]. But as wetland quantity decreases due to natural drought or agriculture drainage, the breeding habitat resource is limited and density-dependent regulation in population growth occurs [21]. On the other hand, the forested habitats in which black ducks breed represent a much more stable ecosystem, prompting a case study question: *What large-scale changes on the breeding grounds could be driving black duck declines?*

The increase in mallards in the black duck range was certainly one potential cause for concern. The mallard range, initially restricted to the central northern prairies, had been expanding into the range of the east coast black duck since at least the 1940s [22, 23]. The historical range of the black duck spanned much of the Atlantic Coast, from North Carolina north to Newfoundland, as well as the Great Lakes states. It was hypothesized that extensive logging across the eastern United States paved the way for eastward expansion of the prairie-adapted mallard [23], supplemented by game farm mallards released for hunting [24]. Regardless of mechanism, by the 1960s and 1970s, mallards outnumbered black ducks on both the breeding [18] and some wintering grounds [23, 25]. There were two obvious consequences of this emergent sympatry, leading a refinement of the case study question: *Is hybridization and/or increased competition with mallards driving the decline of the black duck?*

Interestingly, despite the limited genetic tools of the day, hybridization (as determined through intermediate morphologies) received attention first, perhaps because extensive field studies of competition were more difficult to undertake. Hybridization and loss of pure black duck phenotypes/genotypes was flagged as a concern as early as the 1960s [25], and the first study using allozyme electrophoresis went so far as to conclude that black ducks were merely a melanistic color morph of mallards [26]. This drew the ire of many in the taxonomic community [27], but genetic questions were impossible to fully resolve until recently. The most recent evidence shows that while mallards and black ducks are genetically distinct at mitochondrial markers (which are neutral and diverge rapidly), they are indistinguishable at nuclear introns. However, the weight of evidence for this similarity falls on recent divergence and incomplete lineage sorting, rather than introgression from secondary contact (hybridization) [28]. Furthermore, there is emerging evidence that 40% of "hybrids" as identified by wing morphology are actually genetically pure mallards or black ducks (P. Lavretsky, unpublished data), calling into question historical studies using morphological indices of hybridization.

The narrative of extensive hybridization and loss of the pure black duck lineage prompted studies on pre- and postmating mechanisms that could reinforce isolation of mallards and black ducks as separate species. Genetic compatibility between mallards and black ducks is high [28], and so there are few plausible postzygotic reinforcement mechanisms [29]. In terms of prebreeding mate selection, field studies in southern Ontario showed that while both species exclusively formed intraspecific pairs at the start of the season, after all female mallards were paired, male mallards were able to successfully outcompete male black ducks to mate with unpaired female black ducks [8]. This was in accordance with captive trials that showed female preference for intraspecific mates in isolation, but preference for the dominant mallard males in open trials [30]. Evidently, prebreeding isolation is weak and dependent on the relative densities of mallards and black ducks—not good news for black ducks when mallard numbers are increasing.

We turn now to the second part of the case study question: *Knowing that mallards are competitively dominant to black ducks in captive trials, could they also be forcing black ducks out of optimal breeding territories?* There are two nonmutually exclusive mechanisms by which this might occur: either through competitive dominance or simply by virtue of an increasing and mallard population in the black duck range. Seymour used 18 years of data (1972–1990) on mallard and black duck territorial aggression and reported two instances (out of 14 such encounters) where mallards successfully displaced a black duck pair from a wetland on which they were already resident [31]. More typically, the resident pair succeeded in repelling an intruding pair, regardless of the species of either [31]. That being said, mallards and black ducks tend to favor the same types of wetlands (in terms of physical and biogeochemical attributes) [32]. Using aerial survey data from Ontario going back to the 1970s, Merendino et al. found that mallards appeared on the most fertile wetlands first (sometimes sharing them with black ducks), and eventually black ducks were no longer detected on those high-quality breeding habitats [33]. But, as McAuley et al. point out, a snapshot occupancy survey from the air in no way identifies which species eventually "wins" possession of that wetland [34]. In fact, McAuley et al. analyzed >300 h of observational data and found that black ducks never lost when they initiated an aggressive encounter, whereas when mallards initiated the interaction, black ducks displaced the aggressors or at least shared the wetland 36% of the time [35]. Petrie et al. found that the mere presence of mallards was enough to displace black ducks from wetlands; that is, even if mallards and black ducks were competitively equal, increasing mallard populations would lower carrying capacity for black ducks. Petrie et al. also evaluated the presence of broods on wetlands, and they found a strong inverse relationship between the number of mallard broods and the number of black duck broods [36]. Finally, Maisonneuve et al. found that while mallards will nest in almost any habitat, black duck pairs tend not to breed in the increasingly fragmented agricultural landscapes that have come to dominate southern Canada [37].

Mallard and black duck interactions on the breeding grounds are complex and likely context- and region-dependent. It remains unclear to what extent mallards physically outcompete black ducks for high-quality breeding sites, but most researchers would concede that this does happen [33]. Nevertheless, the mere presence of mallards can preclude wetland occupancy by black ducks if they view them as conspecifics already occupying that territory [36], so the sheer increase of mallards could reduce available wetlands for breeding black ducks. The overall loss, degradation, and fragmentation of black duck breeding habitat has probably also contributed to population decline, but is difficult to quantify. Unfortunately, there are few options for remedying these threats on the breeding grouds: contiguous forested wetlands have been permanently fragmented with agriculture, and there are no straightforward management actions that can ameliorate competition with mallards. With no obvious options to pursue in terms of breeding grounds management (aside from protecting what remains), attention again turned southward.

Wintering Grounds Carrying Capacity

Researchers have increasingly noted the importance of cross-seasonal effects in waterfowl: conditions on the wintering grounds can influence the timing of migration and body condition, which in turn affects productivity on the breeding grounds [38]. In the case of black ducks, the coastal salt marsh they rely on during winter is being lost, fragmented, and degraded by sea level rise, severe storms, and habitat conversion [39], possibly leading to an overall reduction in habitat carrying capacity or cross-seasonal effects on productivity. These losses may be partially offset by gains in habitat further north that are associated with a warming climate and more ice-free days, but these forecasts are still uncertain [40]. Wherever wintering distributions may shift in the future, it is important to address a final case study question: *Are black duck populations limited by habitat and resources available to them on the wintering grounds?*

During the nonbreeding period, food is assumed to be the limiting factor for waterfowl populations [41]. Therefore, managers are primarily concerned with providing enough habitat of a given foraging value to support a target population of ducks over the winter [42]. Black ducks do not strongly avoid roads or urban areas during winter [43], so all habitat is considered functionally available. Bioenergetic models are the primary tool employed by conservation planners to estimate habitat carrying capacity based on energy demand and food supply in different wetland types. Bioenergetic carrying capacity is represented as the available duck-use days (DUD) or the number of days that a habitat can support a single duck based on available food energy and energy demand. It is estimated by:

$$\mathrm{DUD} = {}^{\mathrm{E}}\!/_{\mathrm{DEE}}$$

where E represents energy supply (kcal) and DEE represents daily energy expenditure (kcal/duck/day). Energy supply estimates can be obtained by soil core, nekton, and vegetation sampling, extrapolated to landscape scales using habitat information in a Geographic Information System [44]. Daily Energy Expenditure can be estimated from behavioral analysis [45] using the formula:

$$\mathrm{DEE} = \sum_{h=1}^{n} \sum_{i=1}^{n} \left[\left(\left(\mathrm{RMR} \times a_i\right) + \mathrm{CT}\right) \times T_i\right]$$

where RMR represents the species-specific resting metabolic rate (kcal/bird/h) [46], a_i represents the activity-specific multiplier of RMR for a given behavior [47], CT represents the cost of thermoregulation (kcal/bird/h) [48], and T_i represents the proportion of time spent in a given behavior. Alternatively, if these fine scale data are not available, simply multiplying RMR by 3 seems to provide satisfactory estimates of DEE [46, 49]. From there, managers need to estimate migration chronologies and species-specific population abundance to determine whether energetic supply can satisfy energetic demand for the entire winter.

There have been numerous recent examples of an attempt to estimate energetic carrying capacity. Fino et al. collected soil core samples from forested wetlands on Prime Hook National Wildlife Refuge, Milton, Delaware, in 2014 and Edwin B. Forsythe National Wildlife Refuge, Galloway, New Jersey, USA, in 2015 to estimate food biomass and quantify the energetic capacity of forested wetlands representative of the mid-Atlantic region [50]. They estimated forested wetlands within a 24.1 km distance from the coast provide between 103,696,524 and 192,678,224 DUD supporting 489,135–908,860 black ducks over the 212 days of winter [50]. Livolsi estimated the energetic carrying capacity across all habitat types in Delaware for all species of dabbling ducks [51]. Combining estimates for DEE and food energy, they estimated 8.73×10^6–7.06×10^7 DUD currently available over the winter period. They further extrapolate how sea level rise might impact this energy availability over the next century, and they found dabbler carrying capacities are likely to decrease under all but the most conservative SLR scenarios, due to the gradual replacement of high-energy-density natural habitat (i.e., low marsh, high marsh) with low-energy-density habitat (i.e., subtidal, mudflat).

Ringelman et al. [52] used detailed data previously collected on wintering waterfowl at Edwin B. Forsythe National Wildlife Refuge and created a local model of carrying capacity. They used 1,223 core samples collected between 2006 and 2015 to estimate food energy supply and species-specific 24-h time-activity data collected between 2011 and 2013 to estimate daily energy expenditure. To estimate population-level energy demand, they used standardized monthly ground-surveys (2005–2014) to create a migration curve, and proportionally scaled that curve to fit aerial survey data. Estimating 923 million kcal available and 3.4 billion kcal demand, they found the refuge could be depleted by mid-November. However, past evidence also showed a constant-supply was possible perhaps from tidal replenishment of resources thus allowing maintenance of the population.

Ringelman et al.'s effort allows for relative assessment of biases and uncertainties in carrying capacity modeling and serves as a framework for identifying critical science needs to improve local and regional waterfowl management planning. More generally, carrying capacity models represent the waterfowl management community's best effort to integrate habitat quality with population goals and provide an important foundation for black duck conservation in the United States.

SUMMARY

The historical decline of the American black duck spurred more than three decades of scientific research on all aspects of the black duck life cycle. The reasons for the black duck decline are multi-faceted and likely include overharvest, increased competition and hybridization with mallards, and habitat loss on the breeding and wintering grounds [16]. Of these, management of black ducks on the wintering grounds has taken priority as of late [41], given ongoing loss of salt marsh habitats [39], and the importance of nonbreeding habitat to overwinter fitness [53] and cross-seasonal effects on breeding demographics [54]. *See carrying capacity exercise.*

CASE STUDY QUESTIONS

1. While such emergency stop-gap measures may have seemed prudent at the time, what science was used to validate these regulations?
2. What large-scale changes on the breeding grounds could be driving black duck declines?
3. Is hybridization and/or increased competition with mallards driving the decline of the black duck?
4. Knowing that mallards are competitively dominant to black ducks in captive trials, could they also be forcing black ducks out of optimal breeding territories?
5. Are black duck populations limited by habitat and resources available to them on the wintering grounds?

AUTHOR CONTRIBUTIONS

KMR and CKW conceived of the idea to use black ducks as a pedagogical case study in wildlife management. KMR and CKW both contributed to the text of this manuscript. KMR designed and wrote the carrying capacity exercise.

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COMPETING INTERESTS

The authors have declared that no competing interests exist.

SPPLEMENTARY MATERIALS

Carrying Capacity Exercise Instructions.docx
Carrying Capacity Data.xlsx
Carrying Capacity Sensitivity Analysis.xlsx

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