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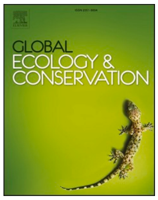

Body mass dynamics in wintering mallards (*Anas platyrhynchos*) in the Lower Mississippi Alluvial Valley

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ABSTRACT

Body mass in overwintering waterfowl is an important fitness attribute as it affects winter survival, timing of spring migration, and subsequent reproductive success. Recent research in Europe and the western United States indicates body mass of mallards (*Anas platyrhynchos*) has increased from the late 1960s to early 2000s. The underlying mechanism is currently unknown; however, researchers hypothesize that increases are due to a more benign winter climate, increased food availability through natural and artificial flooding, introgression of wild mallard populations by game-farm mallards, or shifting of wintering distributions northward. Further investigation of factors related to winter mallard body mass increases and whether this phenomenon is occurring in other major flyways could increase understanding of intrinsic and extrinsic variables influencing waterfowl fitness. Here, we analyzed mallard body mass in the Lower Mississippi Alluvial Valley from 1979 to 2021 to determine sources of temporal variation. We measured hunter-harvested mallards from private hunting clubs, public hunting areas, and duck-plucking businesses. Mallard body mass increased by approximately 6% among all age-sex classes from 1979 to 2021. Average mallard mass increased by about 1.5% per decade but varied substantially among years. Within years, body mass was related to rainfall and river gage height; mallards had greater mass after periods of increased rainfall or river flooding, likely due to increased food availability. Mallard body mass had a marginal negative relationship with severe cold weather (derived using a weather severity index [WSI]). While body mass increased after wet periods within years, there was no relationship of mallard body mass with wet vs dry years, low vs high flood years, or hot vs cold years. Additionally, there was no detectable change in rainfall, river discharge, or temperature from 1979 to 2021. This indicates that rainfall and river height may influence mallard body

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mass within years, but may not be the primary factor responsible for mass increases over time. Our research confirms changes in mallard body mass are widespread and within-season precipitation and flooding account for much of the observed annual variation. Future research investigating specific mechanisms, such as introgression of game-farm mallard DNA and climate change, may clarify their contribution to mallard body mass change over time.

1. Introduction

Long-term monitoring of wildlife has revealed instances of body mass and size change coincident to landscape alterations, climate change, or genetic introgression from captive-bred individuals (Ktitorov et al., 2008; La Sorte et al., 2009; Reeves et al., 2020). For example, changing forestry practices in Norway have been linked to decreases in moose (*Alces alces*) body size from the early 1970s to early 2000s (Lavsund et al., 2003; Bjørneraas et al., 2011). Additionally, the body mass of wood rats (*Neotoma* spp) in New Mexico, USA decreased from 1989 to 1996 as minimum and maximum temperatures increased (Smith et al., 1998). Wacker et al. (2021) demonstrated that farm-raised Atlantic salmon (*Salmo salar*), which escaped and bred with wild salmon, produced a population of larger individuals containing genes from farm stock.

Some of the strongest evidence for body mass change over large time scales comes from waterfowl. For example, Guillemain et al. (2010) showed that the body mass of mallards (*Anas platyrhynchos*) and Eurasian green-winged teal (*Anas crecca crecca*) in Europe increased between 7.3% and 11.7% from the 1960s to the 2000s. They hypothesized that these changes could have been caused by climate change and local habitat management. Waterfowl body mass also has increased over time for several duck species in California, USA, with the authors (Fleskes et al., 2016) indicating that the observed increases might be explained by increases in food resources and wetland area. However, there are other potential explanations, such as stocking programs that use heavier, hand-reared mallards to supplement wild mallard populations, as well as shifts in winter distributions of subpopulations that lead to increased body mass in mallards (Gunnarsson et al., 2011). Given similar trends on different continents, it is likely that the phenomenon of increases in waterfowl body mass over time is occurring elsewhere. Elucidating the extent of these changes is important for understanding how wildlife could be responding to anthropogenic disturbance and a changing world.

Understanding long-term changes in body mass for waterfowl is complicated because mass varies both among and within years in relation to several intrinsic and extrinsic factors. Waterfowl body mass can be affected by endogenous regulation due to life cycle events as well as age and experience. For example, female mallards during mid-pre-breeding molt stage were lower in lipid mass than females in other molt stages (Heitmeyer, 1988). In the same study, females paired with males contained greater lipid masses than unpaired females. Mallard body mass also varies across the wintering period. For example, body mass can increase and peak in midwinter before decreasing prior to spring migration (e.g., Loesch et al., 1992; Guillemain et al., 2010; Fleskes et al., 2016). This trend is most likely driven by physiological processes (Heitmeyer, 1988; Loesch et al., 1992), perhaps as a mechanism to attain optimal spring mass for efficient, fast migration (Lindström and Alerstam, 1992). Other researchers have shown that older ducks have greater body mass because they are more efficient foragers than younger individuals (Hohman and Weller, 1994).

Waterfowl body mass also can be affected by exogenous factors such as food availability and climate. Mallards, like other dabbling ducks, forage in shallow marshes, flooded fields, and floodplains for aquatic invertebrates, waste grain, mast, and seeds of moist-soil plants (Delnicki and Reinecke, 1986; Reinecke et al., 1989; Miller et al., 2003). Because body mass reflects energy acquisition (Labocha and Hayes, 2012), the quality and quantity of available food influences mass dynamics (Rave and Baldassarre, 1991). Food availability for dabbling ducks varies across the winter period as foods are depleted, decompose, or availability is affected by changes in rainfall and flooding (Pöysä, 1983; Hagy and Kaminski, 2012; Behney, 2020). Temperatures can further affect duck body mass by making food less available or by imposing thermal stress that increases metabolism (McKinney and McWilliams, 2005; Schummer et al., 2010).

Here, we assess body mass trends in hunter-harvested mallards across four decades (1979–2021) within the Lower Mississippi Alluvial Valley (LMAV). Our goal was to determine if mallards have increased in body mass and explore other factors related to changes in body mass within and among years. Our specific objective was to quantify variation in winter body mass of mallards in the LMAV in relation to intrinsic factors such as age and sex, and extrinsic factors such as temperature, rainfall, river gage height, day, and year. We hypothesized that mean mallard body mass increased over time as reported in other regions (Guillemain et al., 2010; Gunnarsson et al., 2011; Fleskes et al., 2016), but decreased within winters as ducks prepared for migration and food resources became depleted (Lindström and Alerstam, 1992; Manley, 1999). Additionally, we predicted that mallard body mass would vary substantially within years in response to local weather and river flooding. Because increased water levels can increase access to food resources, we hypothesized that mallards would be heavier with increased winter rain and river flooding (Heitmeyer and Fredrickson, 1981; Delnicki and Reinecke, 1986; Reinecke et al., 1988). We also hypothesized mallards would be heavier when winter weather was mild relative to severe cold, because colder temperatures can induce physiological stress and reduce food availability (Whyte and Bolen, 1984; McKinney and McWilliams, 2005; Schummer et al., 2010).

2. Methods

2.1. Study area

The LMAV is the largest floodplain in the United States and spans 10 million ha across portions of seven states within the Mississippi

Flyway (Reinecke et al., 1989). The LMAV is made up of many river systems used by waterfowl during the nonbreeding period (Bellrose, 1976). Additionally, the LMAV contains rich alluvial soil that makes it a productive agricultural region for crops like rice (*Oryza* spp.) that are a valuable waterfowl food source (Nelms et al., 2007; NFWF, 2019). Our study area comprised the entirety of the

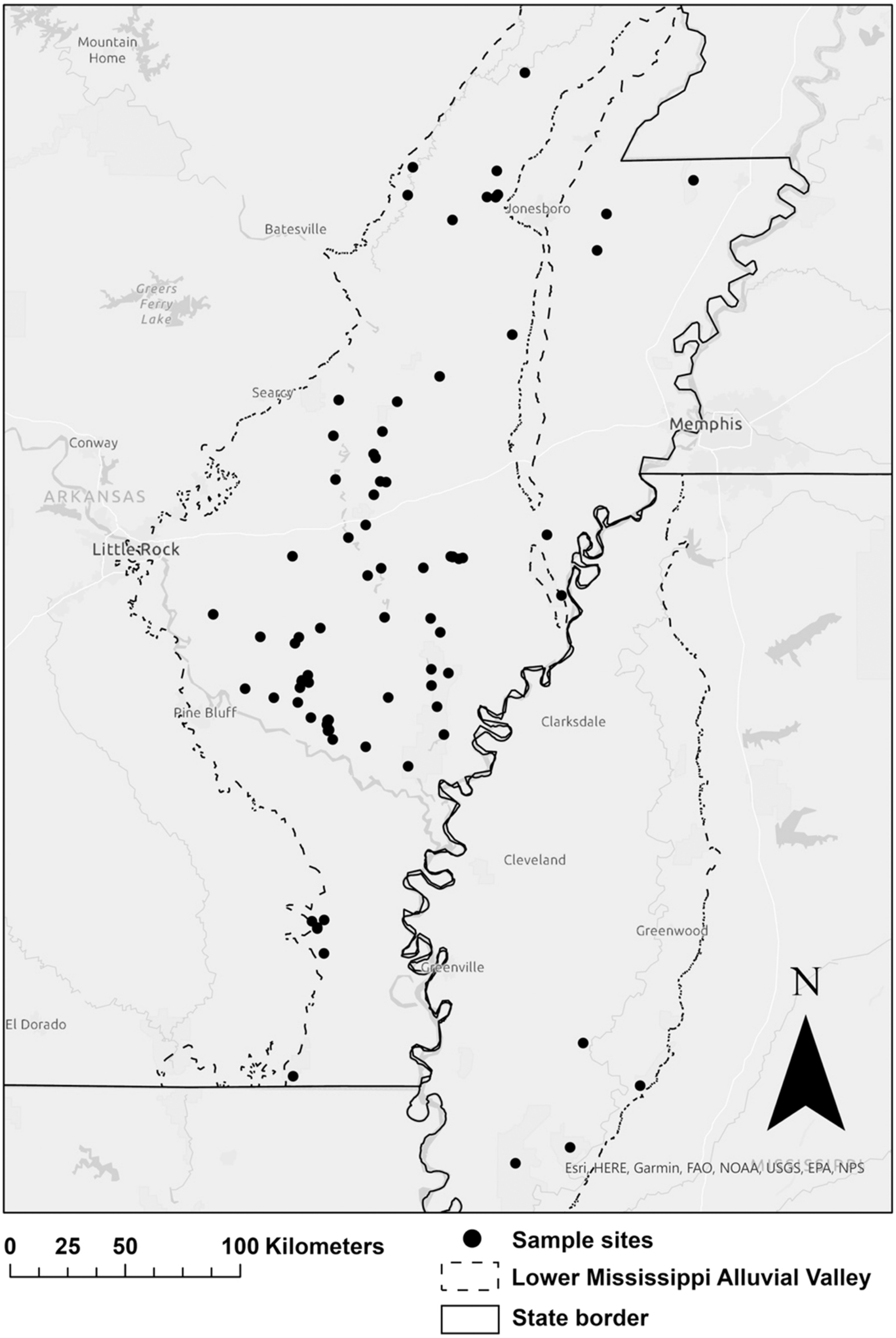

Fig. 1. Map of field sites where body mass measurements were taken from mallards (*Anas platyrhynchos*) across the Lower Mississippi Alluvial Valley of Arkansas and Mississippi from 1979 to 2021.

LMAV of Arkansas, as well as scattered sites within the LMAV in Mississippi (Fig. 1).

2.2. Body mass measurements

We compiled body mass measurements from several different published studies (Delnicki and Reinecke, 1986; Dabbert et al., 1997; Dabbert and Martin, 2000) as well as from data the authors have collectively accumulated from 1979 to 2021. Thus, sample sites and methods varied somewhat across periods. We included body mass measurements of mallards collected during the Mississippi duck hunting seasons of 1979–1980 through 1982–1983, as well as Arkansas duck hunting seasons of 1990–1991, 1999–2000 through 2003–2004, 2015–2016, 2016–2017, 2019–2020, and 2020–2021. Although study sites varied among periods, most study sites were relatively in the same geographic proximity of the LMAV. Therefore, for consistency, we did not include measurements from additional states in more recent years. We collected data from public and private lands, as well as from duck cleaning businesses. In sample years 1979–1980 through 1982–1983 and 1999–2000 through 2003–2004, esophageal contents were removed from waterfowl before measurements were made. In sample years 1990–1991, 2015–2016, 2016–2017, 2019–2020, and 2020–2021 waterfowl were weighed without the removal of esophageal contents. However, in sample years 2019–2020 and 2020–2021, the amount of food in the esophagus was estimated (none [0 g], small [0–20 g], or large [>20 g]) through palpation. Waterfowl in the "large" amount category were removed from analyses. Additionally, in all study years, we excluded mallards with missing limbs, body parts, or birds that contained excessively wet feathers.

In most recent sample years (2019–2020 and 2020–2021), we collected body mass measurements using a stratified sampling design. We divided the Arkansas LMAV into thirds (North, Central, and South) and collected measurements from harvested ducks across as wide a geographic range as possible within each stratum. During the 2020–2021 duck hunting season, we prioritized samples from areas not previously visited in 2019–2020, but also collected data from locations sampled in previous years when available. Body mass measurements from 1979 to 1983 were collected by Delnicki and Reinecke (1986), and measurements from 1990 to 1991 (including both live and harvested samples) were collected by Dabbert et al. (1997) and Dabbert and Martin (2000) (Table 1). From 1979–1980 through 1982–1983, we measured hunter-harvested mallards at Hillside National Wildlife Refuge (NWR), Panther Swamp NWR, Delta National Forest, and private hunting clubs in Holmes, Humphreys, Sharkey, and Yazoo Counties in west-central Mississippi. In 1990–1991, we measured live-captured mallards and mallards harvested from Bayou Meto Wildlife Management Area (WMA) and White River NWR. From 1999–2000 through 2003–2004, we obtained body mass data for mallards at a duck cleaning business in Stuttgart, Arkansas in the Grand Prairie region within the central Arkansas MAV. During 2015–2016 and 2016–2017, we collected measurements from mallards harvested on private farmland in east-central Arkansas. During 2019–2020 and 2020–2021, we collected mallard body mass measurements from harvested mallards on private land and public waterfowl hunting areas (WMAs and NWRs) across the north, central, and south LMAV of Arkansas. Mallards were aged and sexed using plumage dimorphism and feather morphology (Krapu et al., 1979; Carney, 1992).

2.3. Variables for statistical modeling

To analyze age and sex differences among and within years from 1979 to 2021, we categorized each mallard into one of four classes

Table 1
General locations; sample period; land use types (state owned Wildlife Management Areas (WMA's), Federally owned National Wildlife Refuges (NWRs), private land, and businesses that plucked harvested ducks for hunters); and weight scale, body mass correction, and aging methodology of harvested or live mallards (*Anas platyrhynchos*) within the Lower Mississippi Alluvial Valley during study years 1979–1983, 1990–1991, 1999–2004, 2015–2017, 2019–2021. N/A (not applicable) indicates no food correction was necessary.

Sample years	1979–1983	1990–1991	1999–2004	2015–2017	2019–2021
States sampled	Mississippi	Arkansas	Arkansas	Arkansas	Arkansas
Duration of hunting seasons sampled	December & January	November – February	December & January	*2015–2016:* December & January *2016–2017:* November – January	November – February
Source of ducks	National Wildlife Refuges, National Forest, Private Land	Wildlife Management Areas and National Wildlife Refuges	Duck Plucking Businesses	Private Land	Wildlife Management Areas and National Wildlife Refuges, National Forest, Private Land
Weight measurement device	Spring Scale (nearest 10 g)	Spring Scale (nearest g)	Battery Powered Electronic Balance (nearest g)	Spring Scale (nearest 10 g)	Battery Powered Electronic Balance (nearest g)
Food removed before weighing?	Yes	No	Yes	No	No
If no, how food was corrected?	N/A	Subtracted weight of esophageal contents from raw mass of bird	N/A	N/A	All birds that had large amounts (>20 g) of undigested esophageal contents were removed from analysis

comprised of adult males, adult females, juvenile males, and juvenile females, hereafter referred to as AgeSex. To explore how mallard body mass has changed from 1979 to 2021, we used year as a fixed effect within our models (see Statistical Analyses for more information on model development). Because study years (or duck hunting seasons) span calendar years (often Nov-Feb), for clarity our use of the term "year" refers to the duck hunting season initiating in November of that year and spanning to February of the next calendar year. Days refer to chronological days within hunting seasons. Because hunting season dates varied among years, we represented days within seasons as modified Julian days, with the earliest date that a mallard's mass was measured across the study labeled as day 1 (November 19th) and each subsequent day numbered sequentially until day 83 (Feb 13th), the latest date a bird was measured.

To assess the relationship of cumulative rainfall and cold weather severity (or Weather Severity Index developed by Schummer et al., 2010; WSI) with mallard body mass, we compiled climate data from representative National Oceanic and Atmospheric Administration (NOAA) weather stations. The variables we used were daily cumulative precipitation (cm) and minimum and maximum daily temperature (°C). We obtained data from Yazoo City, Yazoo County, Mississippi (station name: Yazoo City 5 NNE) for winters 1979–1980 through 1982–1983 and from Arkansas (station names: Stuttgart 9 ESE, Des Arc, Searcy, Georgetown, Pine Bluff, Augusta, Wynne, Alicia, Keiser, Eudora, Monticello Municipal Airport, Marianna, Arkansas Post, Rohwer, Paragould, and Pocahontas) for winters 1990–1991, 1999–2000 through 2003–2004, 2015–2016, 2016–2017, 2019–2020, and 2020–2021 based on proximity of sampling sites and weather stations. We recognize that daily rainfall on a given date may not be the best measure of how precipitation influenced body mass on the date of harvest. Because the known movement of waterfowl before measurement of body mass was unknown, and it can take waterfowl anywhere from 8 to 72 h to digest most food resources (Charalambidou et al., 2005), we calculated a 3-day cumulative rainfall before the dates of mallard measurement to more accurately represent the relationship between precipitation and mallard body mass. Similarly, we did not use in our analysis the daily average temperature from the day that a bird was measured. Instead, we calculated daily average temperatures for each day and season and used these values to calculate a 3-day mean of daily average temperatures before mallards were measured. Finally, we calculated WSI using our 3-day mean temperatures (by modifying the WSI equation from Schummer et al., 2010) to evaluate the relationship of weather severity and mallard body mass. We modified the WSI equation to use three-day means rather than two-week means because we wanted to represent cumulative effects of temperature experienced by ducks more recently before measurement (Eq. (1)).

$$\begin{aligned} WSI = \; & (-1 * Average\ of\ Previous\ \ 3-day\ Average\ \ Daily\ Temperature(C^{\circ})) \\ & + (Number\ \ of\ Days\ \ Consecutively \leq 0\ \ C^{\circ}) \\ & + (Snow\ Depth\ (cm\ *\ 0.394)\ on\ Day\ of\ Harvest) \\ & + (Consecutive\ days \geq 2.54\ cm\ \ of\ \ snow) \end{aligned} \tag{1}$$

Finally, we used river gage height (m) data as a function of flooding. River gage height values were identified using associated discharge (cfs) values from rate tables obtained from the USGS Lower Mississippi-Gulf Water Science Center for Mississippi winters 1979–1983 (gage name: Big Black River near Bovina) and for Arkansas winters 1990–1991,1999–2000 through 2003–2004, 2015–2016, 2016–2017, and 2019–2020, and 2020–2021 (gage names: Black River near Corning, Black River at Pocahontas, Black River at Black Rock, Cache River at Egypt, White River at Newport, White River at Georgetown, Cache River near Cotton Plant, White River at DeValls Bluff, L′Anguille River near Colt, L′Anguille River near Palestine, Bayou Meto near Lonoke, Bayou Bartholomew at Garrett Bridge, and Bayou Bartholomew near McGehee). We collected data from river gages nearest our sample sites to examine the relationship of daily river height to mallard body mass. Similar to rainfall, we expected mallard body mass would be greater when river levels were higher because of increased foraging habitat. Importantly, we found rainfall and river gage height were not highly correlated (Pearson Correlation [r] = 0.25). This result may indicate that rivers can fluctuate from rainfall upstream of areas absent of local rainfall or by human control (e.g., locks, dams, levees) (Junk et al., 1989; MRC, 2007). Additionally, forage availability may reflect different combinations of rainfall and river flooding. Rainfall may be more influential in flooding habitat not connected to or near river systems (e.g., puddling or ponding), whereas river flooding more likely to provides access to foraging habitat in riparian and adjacent overbank habitats (Smith and Callahan, 1983; Galat et al., 1998, Heitmeyer, 2006).

2.4. Statistical analyses

To investigate mallard body mass change over time and in response to intrinsic and extrinsic factors, we used linear mixed effects models (LMMs) in R Computing Software (R Core Team 2020) using the *lme4* package (Bates et al., 2015). We analyzed five separate LMMs each including the interactive effect of AgeSex and one of the fixed factors (year, day of season, cumulative rainfall, river gage height, and WSI) to isolate the effects of age and sex on the relationships of body mass and fixed factors. Mallard body mass was the response variable in all models, and we used location as a random variable to control for variation across sites. After developing all variables, we checked for collinearity among predictor variables using Pearson's correlation coefficient. No predictor variables were highly correlated ($\geq$ 0.7 correlation), so all were retained for analyses (Dormann et al., 2013). Linearity and homogeneity of responses to each predictor variable were assessed using residual plots. To better meet assumptions of linearity, river gage height and cumulative rainfall were log transformed (Quinn and Keough, 2002); all other variables met model assumptions. Model goodness-of-fit was evaluated using residual plots as well as likelihood-ratio tests described by Liang and Yang (2022) (see Table S1-S5 in Supporting Information). To facilitate interpretation of relationships between body mass and fixed factors, figure axes were back-transformed when necessary. Relationships were evaluated using $\alpha < 0.05$, parameters are presented with $\pm$ 95% confidence intervals (CI), and means presented in the Results section include $\pm$ standard error (SE).

Given that our initial analyses showed correlations between body mass and some climate variables, we then used broader scale analyses to explore if some climate variables had changed during the duration of this study. We also explored analyses to determine how mallard body mass may have correlated with these variables calculated on an annual scale. We compiled daily rainfall (cm), daily discharge (cfs), and daily average temperature (C°) data from four weather stations (station names: Jonesboro 2 NE, AR; Pine Bluff, AR; Greenville, MS; Greenville Asos, MS) and four river gages (gage names: Black River near Corning, AR; Bayou Meto near Lonoke, AR; Bayou Bartholomew near McGehee, AR; Bayou Bartholomew near Garret Bridge, AR) distributed across North, Central, and South Arkansas and Mississippi in the LMAV to represent average rainfall, habitat conditions, and climate across the broader LMAV landscape. Discharge data was used rather than river gage height data for broader scale climate analyses because we had access to more daily discharge data for each year from 1979 to 2021 for river gages spread across the LMAV. We also note that discharge data and river gage height are related, as discharge data is used to identify river gage height values for each gage using rate tables. Using methods adapted from Nichols et al. (1983), we calculated annual deviance from long-term average cumulative rainfall and long-term average river discharge, as well as annual deviance from long-term average temperature. We considered as "wet years" those that deviated positively from the average cumulative rainfall from 1979 to 2021 and "dry years" as those that deviated negatively. For river discharge, we considered "high years" as those that deviated positively from average river discharge from 1979 to 2021 and "low years" as those that deviated negatively. For temperature, we considered "hot" years as those that deviated positively from average temperature from 1979 to 2021 and "cold" years as those that deviated negatively. We then performed three sets of four nonparametric Kruskall-Wallis tests to determine if wet or dry years, high or low river years, as well as hot or cold years were related to average annual body mass for each age and sex class. To determine how rainfall, discharge, and temperature changed over the 42 years of our study, we conducted three separate simple linear regressions with deviations as the response variable and year as the independent variable.

2.5. Determining rate of change (%) of body mass over time

To quantify rate of change in body mass in a manner comparable to previous investigations (Europe and California, USA; Guillemain et al., 2010; Fleskes et al., 2016) and to facilitate comparisons, we pooled duck body mass within each AgeSex into decadal groups and calculated the rate of change in body mass between groups. We used the following time periods: Decade 1 = 1979–1980 through 1988–1989, Decade 2 = 1989–1990 through 1998–1999, Decade 3 = 1999–2000 through 2008–2009, Decade 4 = 2009–2010 through 2018–2019, and Decade 5 = 2019–2020 through 2020–2021. We chose to pool body mass measurements among decades because we collected data during sampling periods separated by unequal gaps of time. We then calculated pair-wise changes in average body mass across decades using variations of the following rate of change equations (Hopkins, 1992, Eqs. (2) and (3)):

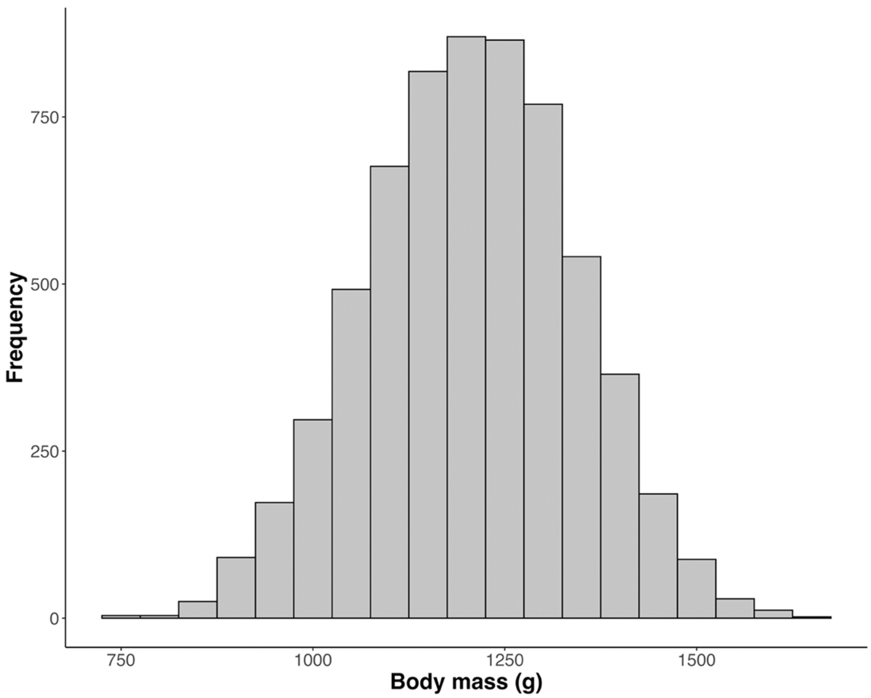

Fig. 2. Frequency and resulting distribution of body mass measurements taken from mallards (*Anas platyrhynchos*) across the Lower Mississippi Alluvial Valley of Arkansas and Mississippi from 1979 to 2021.

$$\%Average\ \ Body\ \ Mass\ \ Growth\ \ Between\ \ Individual\ \ Decades = \left(\frac{Avg.Body\ \ Mass\ \ Decade\ \ (D) - Average\ \ Body\ \ Mass\ \ of\ \ Previous\ \ Decacde\ (D-1)}{Average\ \ Body\ \ Mass\ of\ \ Previous\ \ Decade\ (D-1)}\right) * 100 \quad (2)$$

$$\%Average\ \ Body\ \ Mass\ \ Growth\ \ per\ \ Decade = \frac{Sum\ \ of\ \ \%\ \ Change\ \ Between\ \ All\ \ 5\ Chronological\ \ Decade\ \ Pairs\ \ (1\ \&\ \ 2, 2\ \ \&\ \ 3, etc.)}{5} \quad (3)$$

For clarification, we pooled body mass measurements by decade only to calculate mean rates of change of body mass over time; pooling was not done when analyzing variation in body mass with LMMs.

3. Results

During 1979–2021 we measured body mass of 6307 mallards within the LMAV (Fig. 2) including 2765 adult males, 1505 juvenile males, 912 adult females, and 1125 juvenile females. Mean mallard mass was highest in sample year 2020–2021 among most age-sex classes (adult males = 1331.28 g ± 4.89, adult females = 1180.79 g ± 11.93, juvenile males = 1290.50 g ± 4.97) except for juvenile females, which were slightly heavier in 2015–2016 (1141.1 g ± 27.01). Adult male (1167.22 g ± 13.53) and juvenile female (988.86 g ± 33.02) mallard body mass was lowest during 2016–2017. Juvenile male body mass was lowest in 1990–1991 (1034.00 g ± 9.00) and adult female mass was lowest in 1980–1981 (1051.15 g ± 6.57) (Table 2).

3.1. Body mass change over time

Mallard body mass varied among years ($t_{113} = 4.04$, P < 0.001), with increases in mass occurring from 1979 to 2021 (β = 1.43, confidence interval [CI] = 0.72 – 2.13). All age and sex classes increased in mass over the 42-year period (Table 3 and Fig. 3), although consistent differences remained among age and sex classes. On average, the rate of change of mass from Decade 1 to Decade 5 was 5.57% (69.48 g) for adult males, 6.87% (75.17 g) for adult females, 7.63% (90.12 g) for juvenile males, and 7.55% (78.55 g) for juvenile females. The mean rate of change of body mass per decade was 1.22% (13.89 g) for adult males, 1.48% (15.03 g) for adult females, 1.90% (18.02 g) for juvenile males, and 1.50% (15.71 g) for juvenile females.

Although mallard body mass of sampled mallards increased over the duration of the study, body mass also varied with days within years ($t_{6223} = -8.29$, P < 0.001). Mallard body mass decreased from the start to end of each hunting season (β = −0.97, CI = −1.20 to −0.74). The rate of decline in body mass was higher for adults than juveniles (Table 3 and Fig. 4).

3.2. Body mass in relation to climate within seasons

Mallard body mass was related to 3-day cumulative rainfall ($t_{6306} = 5.97$, P < 0.001), with body mass increasing as cumulative rainfall increased (β = 4.78, CI = 3.21 – 6.34). Despite differences in mass among AgeSex, all AgeSex classes increased curvilinearly with cumulative rainfall (Table 3 and Fig. 5).

We also observed that mallard body mass was related to river gage height ($t_{5971} = 4.20$, $P < 0.001$), with body mass increasing as river gage height increased (β = 19.54, CI = 10.43 – 28.65). This trend also was positive and curvilinear among all age and sex classes (Table 3 and Fig. 6). There was a marginal ($t_{6237} = -1.94$, $P = 0.053$), but negative relationship (β = −0.96, CI = −1.92 to 0.01)

Table 2
Average body mass (rounded to nearest gram; standard error [SE] rounded to nearest integer) and sample size from mallards (*Anas platyrhynchos*) within the Lower Mississippi Alluvial Valley among hunting seasons in years 1979–1983, 1990–1991, 1999–2004, 2015–2017, 2019–2021.

	Males						Females					
	Adults			Juveniles			Adults			Juveniles		
Year	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*
1979–1980	1262	7	207	1220	12	71	1114	13	52	1088	12	64
1980–1981	1205	5	459	1134	13	64	1051	7	182	1001	10	82
1981–1982	1240	5	390	1144	25	18	1112	9	122	1004	21	26
1982–1983	1319	6	253	1239	24	16	1145	10	97	1101	26	16
1990–1991	1205	26	20	1034	9	2	1168	20	31	1068	36	13
1999–2000	1262	8	168	1173	9	118	1111	11	109	1029	8	122
2000–2001	1261	11	116	1205	8	111	1109	12	66	1053	9	115
2001–2002	1282	11	87	1216	14	41	1181	15	45	1070	11	76
2002–2003	1288	12	76	1228	13	48	1155	14	49	1082	13	49
2003–2004	1280	12	86	1209	13	55	1136	18	26	1037	10	74
2015–2016	1299	21	29	1253	21	29	1103	36	9	1141	27	10
2016–2017	1167	14	59	1164	19	24	1057	37	13	989	33	14
2019–2020	1299	5	391	1253	5	455	1158	12	53	1095	7	219
2020–2021	1331	5	424	1290	5	453	1181	12	58	1140	7	245
All Years	1270	2	2765	1241	3	1505	1118	3	912	1077	3	1125

Table 3
Results from linear mixed effects models evaluating the influence of year, day of season, cumulative rainfall, gage height, and Weather Severity Index (WSI) on the body mass of mallards (*Anas platyrhynchos*) among age and sex classes from 1979 to 2021 in the Lower Mississippi Alluvial Valley of Arkansas and Mississippi (* denotes a statistically significant relationship between variable and body mass). AF represents adult females, JM represents juvenile males, and JF represents juvenile females.

Model	Variable	t	P	β (95% CI)
Year x AgeSex	Year *	$t_{113} = 4.04$	< 0.001	1.43 (0.72 – 2.13)
	AF *	$t_{6257} = -26.02$	< 0.001	-149.05 (-160.27 to -137.82)
	JM*	$t_{6253} = -10.31$	< 0.001	-78.95 (-93.96 to -63.94)
	JF*	$t_{6262} = -29.35$	< 0.001	-214.47 (-228.80 to -200.15)
	Year:AF	$t_{6266} = 1.36$	0.17	0.37 (-0.16 to 0.90)
	Year:JM *	$t_{6291} = 3.57$	< 0.001	0.84 (0.38 – 1.30)
	Year:JF	$t_{6289} = 1.59$	0.11	0.39 (-0.09 to 0.87)
Day x AgeSex	Day *	$t_{6223} = -8.29$	< 0.001	-0.97 (-1.20 to -0.74)
	AF *	$t_{6280} = -10.85$	< 0.001	-123.39 (-145.69 to -101.09)
	JM*	$t_{6286} = -8.14$	< 0.001	-77.17 (-95.76 to -58.58)
	JF*	$t_{6281} = -23.61$	< 0.001	-230.95 (-250.12 to -211.77)
	Day:AF	$t_{6292} = -1.84$	0.066	-0.40 (-0.84 to -0.027)
	Day:JM*	$t_{6277} = 2.54$	0.011	0.47 (0.11 – 0.83)
	Day:JF*	$t_{6282} = 2.75$	0.006	0.54 (0.15 – 0.92)
Rainfall x AgeSex	Rainfall*	$t_{6306} = 5.97$	< 0.001	4.78 (3.21 – 6.34)
	AF *	$t_{6245} = -29.07$	< 0.001	-138.89 (-148.26 to -129.52)
	JM*	$t_{6285} = -14.08$	< 0.001	-58.34 (-66.46 to -50.21)
	JF*	$t_{6274} = -45.48$	< 0.001	-204.92 (-213.75 to -196.09)
	Rainfall:AF	$t_{6266} = 1.66$	0.098	2.50 (-0.46 to 5.47)
	Rainfall:JM	$t_{6284} = -1.69$	0.091	-2.22 (-4.79 to 0.35)
	Rainfall:JF	$t_{6265} = -0.03$	0.98	-0.04 (-2.84 to 2.75)
Gage Height x AgeSex	Gage Height*	$t_{5971} = 4.20$	< 0.001	19.54 (10.43 – 28.65)
	AF *	$t_{6267} = -14.21$	< 0.001	-153.06 (-174.18 to -131.94)
	JM*	$t_{6295} = -5.45$	< 0.001	-52.74 (-71.74 to -33.75)
	JF*	$t_{6275} = -21.95$	< 0.001	-229.72 (-250.23 to -209.20)
	Gage Height:AF	$t_{6272} = 1.02$	0.31	7.63 (-7.06 to 22.31)
	Gage Height:JM	$t_{6301} = -0.18$	0.86	-1.24 (-14.91 to 12.44)
	Gage Height:JF*	$t_{6281} = 2.57$	0.010	19.75 (4.71 – 34.80)
WSI x AgeSex	WSI	$t_{6237} = -1.94$	0.053	-0.96 (-1.92 to 0.01)
	AF *	$t_{6251} = -22.62$	< 0.001	-146.31 (-158.99 to -133.63)
	JM*	$t_{6288} = -9.74$	< 0.001	-56.02 (-67.30 to -44.74)
	JF*	$t_{6259} = -34.79$	< 0.001	-213.98 (-226.03 to -201.92)
	WSI:AF	$t_{6269} = -0.43$	0.66	-0.44 (-2.41 to 1.54)
	WSI:JM	$t_{6294} = -0.35$	0.73	-0.27 (-1.81 to 1.27)
	WSI:JF	$t_{6269} = -1.74$	0.082	-1.53 (-3.26 to 0.19)
Null		$t_{81} = 183.6$	< 0.001	1241.53 (1228.24 – 1255.17)

between mallard body mass and WSI, which bears further exploration particularly in regions that experience more severe winter temperatures than the LMAV. Finally, likelihood ratio tests indicated that all models had a better goodness-of-fit than the null model (see Table S1-S5 in Supporting Information).

3.3. Long-term Relationships of Body Mass and Climate

We found no relationship between mean annual body mass and annual deviation from long-term mean cumulative winter rainfall for any AgeSex class: adult males ($H_1 = 0.54$, $P = 0.46$), adult females ($H_1 = 3.74$, $P = 0.053$), juvenile males ($H_1 = 0.22$, $P = 0.64$), or juvenile females ($H_1 = 1.96$, $P = 0.16$). Over the 42-year span of the study, there were more dry years (n = 24) than wet years (n = 18). However, there was no trend in the deviation from average cumulative winter rainfall over the last 42 years ($F_{1,40} = 0.04$, $P = 0.83$).

We also found no relationship between mean annual body mass and annual deviation from long-term mean discharge for any AgeSex class: adult males ($H_1 = 1.63$, $P = 0.20$), adult females ($H_1 = 1.63$, $P = 0.20$), juvenile males ($H_1 = 0.53$, $P = 0.47$), or juvenile females ($H_1 = 0.30$, $P = 0.58$). Over the 42-year span of the study, there were more high river years (n = 40) than low river years (n = 2). However, there was no trend in the deviation from long-term average discharge per winter over the last 42 years ($F_{1,40} = 0.25$, $P = 0.62$).

Finally, we found no relationship between mean annual body mass and annual deviation from long-term average temperature for any AgeSex class: adult males ($H_1 = 1.67$, $P = 0.20$), adult females ($H_1 = 1.35$, $P = 0.25$), juvenile males ($H_1 = 1.07$, $P = 0.30$), or juvenile females ($H_1 = 1.67$, $P = 0.20$). Over the 42-year span of the study, there were more hot years (n = 25) than cold years (n = 17). However, there was no trend in the deviation from long-term average temperature per winter over the last 42 years ($F_{1,40} = 2.72$, $P = 0.12$).

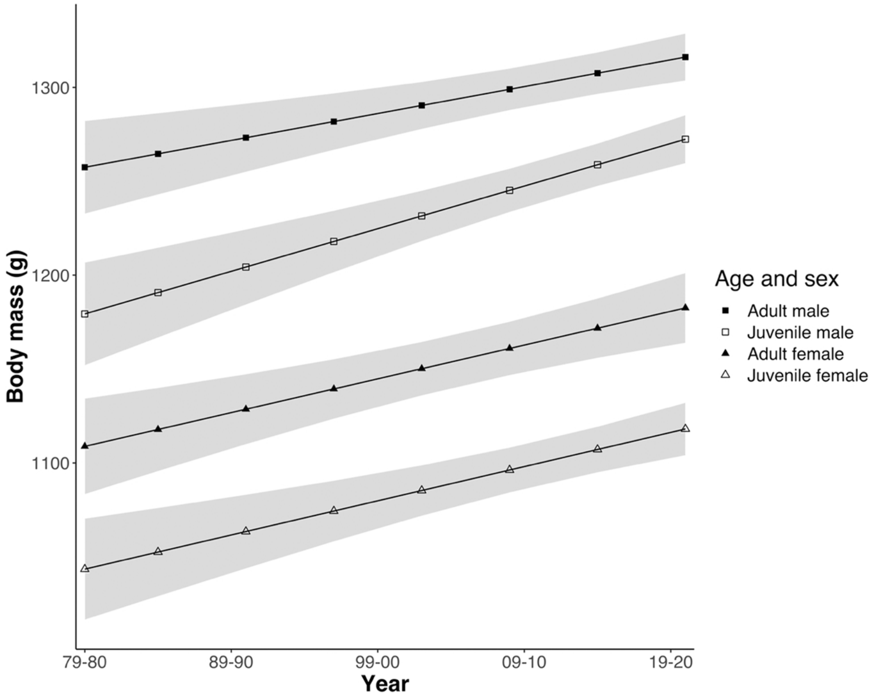

Fig. 3. Predicted relationship of adult male, juvenile male, adult female, and juvenile female mallard (*Anas platyrhynchos*) body mass with year (79–80 = 1979–1980, 89–90 = 1989–1990, 99–00 = 1999–2000, 09–10 = 2009–2010, and 19–20 = 2019–2020) within the Lower Mississippi Alluvial Valley from 1979 to 2021. Solid black lines refer to estimated mean body mass and gray bands are upper and lower limits of the 95% confidence interval (CI).

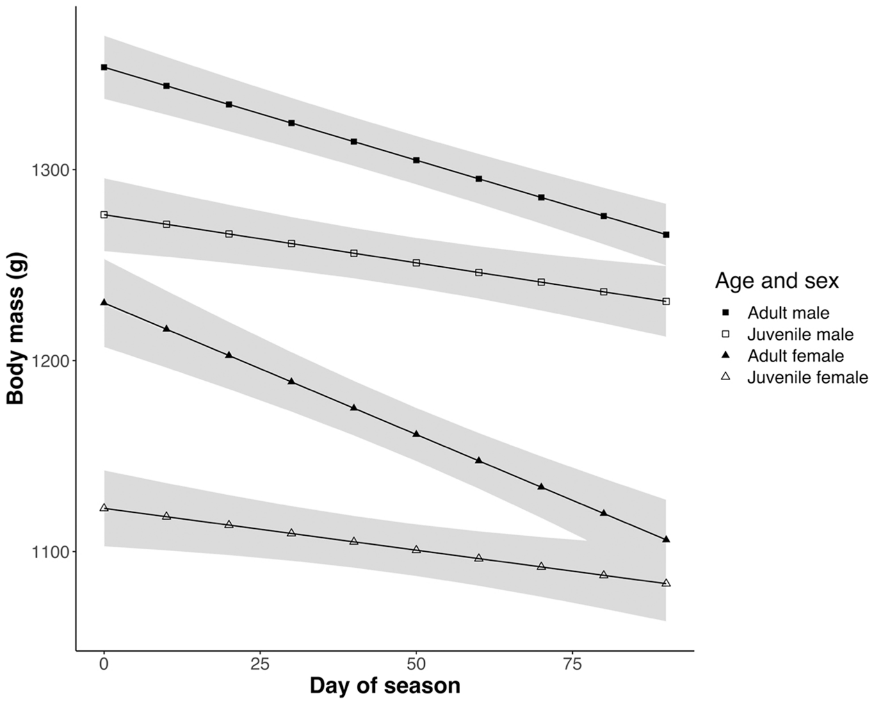

Fig. 4. Predicted relationship of adult male, juvenile male, adult female, and juvenile female mallard (*Anas platyrhynchos*) body mass with day of season within the Lower Mississippi Alluvial Valley from 1979 to 2021. Solid black lines refer to estimated mean body mass and gray bands are upper and lower limits of the 95% confidence interval (CI).

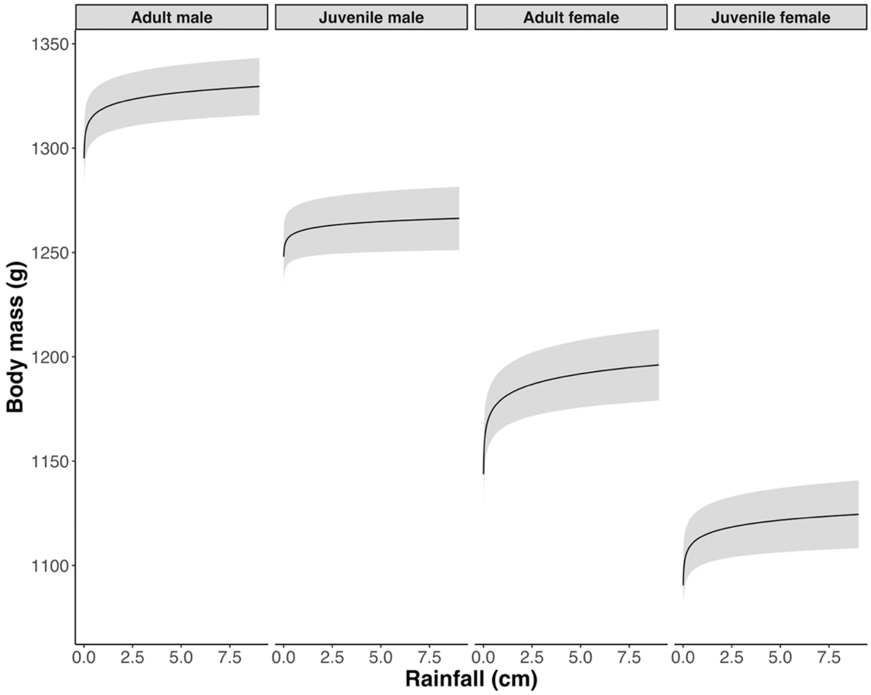

Fig. 5. Predicted relationship of mallard (*Anas platyrhynchos*) body mass with 3-day cumulative rainfall previous to mallard harvest/capture within the Lower Mississippi Alluvial Valley from 1979 to 2021. Solid black lines refer to estimated mean body mass and gray bands are upper and lower limits of the 95% confidence interval (CI).

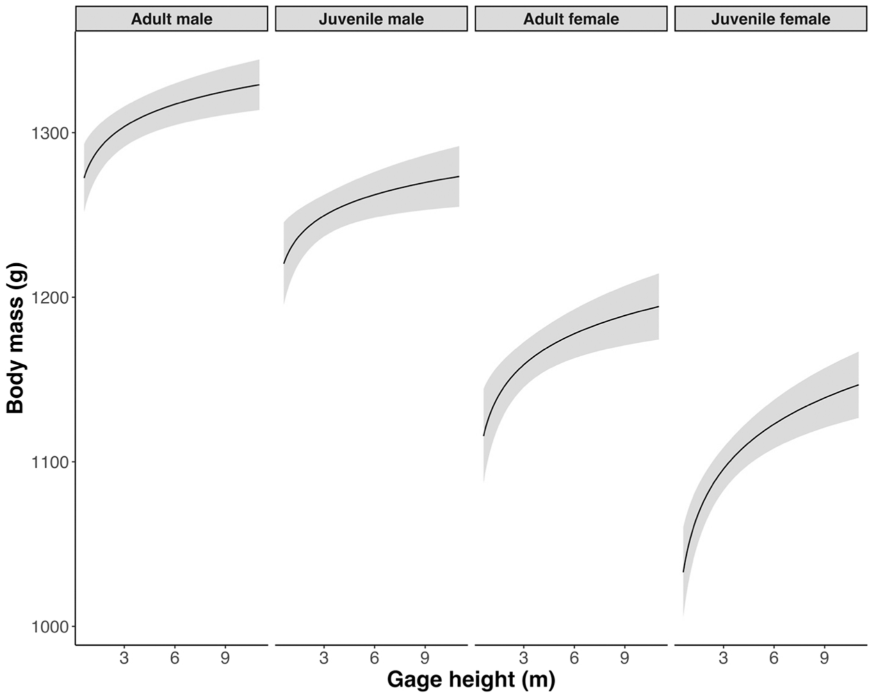

Fig. 6. Predicted relationship of mallard (*Anas platyrhynchos*) body mass with river gage height within the Lower Mississippi Alluvial Valley from 1979 to 2021. Solid black lines refer to estimated mean body mass and gray bands are upper and lower limits of the 95% confidence interval (CI).

4. Discussion

Our study documented increases in mallard body mass in the LMAV from 1979 to 2021. We estimated body mass increases of 5.6–7.6% over all age-sex classes. These magnitudes of change are consistent with increases in body mass observed in both western North America and Europe. In the Central Valley of California, USA during 2006–2008, mallard body mass was 3.2% greater than in 1985–1993, and 6.1% greater than in 1982–1984 (Fleskes et al., 2016). In Europe, mallard body mass increased $\geq$ 7.3% among all age-sex classes collected in 2002–2008 as compared to 1952–1969 (Guillemain et al., 2010).

The body mass of hunter-harvested mallards may underestimate the population body mass (Heitmeyer et al., 1993), but our conclusions about increasing mass over decades and decreasing mass within winters are robust to this effect unless the bias changed systematically over years or within seasons. The decrease of mass within winters is especially robust to this bias because, if hunters gradually removed birds of lower mass during winter, there would be an increasing trend in mass within winters rather than the decreasing trend observed. Further, we acknowledge body mass differences exist among method of harvest (Szymanski et al., 2013) and can change with desiccation time (Van Bröckel, 1973; Clark, 1979). However, our samples were collected from hunters at private or public hunting areas within a few hours of harvest or measured at duck plucking businesses after being delivered by hunters the morning of harvest. Thus, rates of body mass loss due to decay would be similar among samples. Therefore, we believe the patterns observed to be as robust to bias as possible with the use of hunter-harvested mallards.

Although increases in body mass have occurred in multiple regions, the underlying mechanisms have yet to be elucidated. Several potential hypotheses have emerged including climate change, genetic swamping of wild populations with captive bred individuals, wintering distribution shifts, and landscape alteration (Guillemain et al., 2010; Gunnarsson et al., 2011; Fleskes et al., 2016). We explore the four hypotheses that attempt to explain mallard body mass increase over time and then consider changes of mallard body mass within winters.

The effects of climate change, such as increased rainfall, flooding, or warmer temperatures, could explain observed changes in mallard body mass over time. However, our results indicated that average annual winter mallard body mass was not related to the occurrence of wet or dry years or the number of years with high or low river years. Therefore, while short-term changes in winter precipitation can influence winter body mass and following spring productivity in some breeding populations of mallards (Heitmeyer and Fredrickson, 1981; Osnas et al., 2016), long-term trends in rainfall may not be fully responsible for long-term changes in mallard body mass or productivity. Further, there were no identifiable trends in rainfall or river discharge within the LMAV over the last 42 years. Interestingly, recent weather data show that annual winter rainfall and annual river flooding have increased in variability from 1979 to 2021 in the southeast United States, while also indicating that rainfall and river flooding have increased. These increases are predicted to continue in future years (IPCC 2021, NOAA 2021). This increase in variability likely confounded our ability to detect a trend. Because the amount of surface water on the landscape affects the degree to which waterfowl can access food resources (Fredrickson and Taylor, 2007), it is possible that increasing precipitation and river flooding could increase foraging habitat for mallards. Furthermore, our results indicated that average annual winter mallard body mass was not related to the occurrence of hot or cold years. Additionally, there were no identifiable trends in temperature within the LMAV over that last 42 years. We believe that this is due to the LMAV having relatively mild winters and loss of natural variation through averaging of temperature values among years and multiple locations. We note, however, that more large-scale climate analyses indicate that temperatures are increasing in Central North America (IPCC 2021; NOAA 2021). Because cold temperatures and potentially resulting ice and snow can inhibit access to food resources (Schummer et al., 2010), and colder temperatures increase energy required by waterfowl for thermoregulation (McKinney and McWilliams, 2005), it is reasonable to assume that increased temperatures will increase food resources and energy available for maintaining or increasing body mass for wintering waterfowl. On the contrary, we also recognize that warmer temperatures could limit food resources through accelerated maturation or seed germination, as well as increased rates of depredation, decomposition, and molding (Williams and McDonald, 1983; Stafford et al., 2006; Williams et al., 2014). Therefore, the effects of temperature on food resources within the LMAV and how that relates to waterfowl metabolism warrants exploration.

Another hypothesis that might explain the increase in waterfowl body mass is the interbreeding of wild-strain and domestically-derived game-farm mallards. In a recent study, nearly 40% of mallards sampled in the Mississippi Flyway had game-farm mallard DNA signatures (Lavretsky et al., 2019). Several studies have reported game-farm mallards are heavier and larger in size than North American wild-strain mallards (Figley and VanDruff, 1982; Byers and Cary, 1991; Dubovsky and Kaminski, 1994; Svobodová et al., 2020). Thus, over time, progeny of wild-strain and game-farm mallards could exhibit increased mallard body mass. Gunnarsson et al. (2011) showed that, in Europe, mallard body mass increased over a 30-year period when regular mallard stocking occurred. In contrast, Eurasian green-winged teal that were not exposed to stocking programs in Europe did not increase in mass over the same 30-year period. However, while it may be true that game-farm mallard introgression could lead to heavier mallards over time within the LMAV, we recognize the possibility that domestically-derived game-farm mallards in the LMAV may not be heavier than wild-strain mallards; and thus, the opposite effect may occur, which has been observed in other species morphological traits. For example, Groves (1982) found skull size was smaller in captive Indian rhinoceroses (*Rhinoceros unicornis*) as compared to their wild counterparts. In equids (*Equus* spp.), it has been reported that captive individuals have smaller crania than wild strain individuals (Groves, 1966). Researchers have also found that, among rhesus macaques (*Macaca mulatta*), captive-bred individuals do not grow as large as free ranging individuals from the same locality (Gore, 1993). The relationship between mallard body mass and genetics is further complicated by a recent study that assessed the presence of game-farm mallard DNA signatures within the LMAV. Researchers found that only 4% of samples were related to game-farm mallards and suggested the LMAV population of mallards is becoming “wilder” (Davis et al., 2022). If future research finds that domestically-derived game-farm mallards are not heavier than wild-strain mallards, the results from Davis et al. (2022) would indicate the increase in more wild-strain mallards in the LMAV as compared to mallards containing game-farm mallard DNA signatures might explain increases in mallard body mass. Alternatively, if future research finds that wild mallards with game-farm mallard origins are in fact heavier than wild-strain mallards, then it is possible that game-farm mallard genes may not explain mallard body mass increases in the LMAV. Therefore, while the hypothetical effect of domestically-derived mallard stock on wild mallard body mass remains speculative and correlational, we believe it is one of the hypotheses that could be most directly tested.

Shifting wintering distributions could also potentially explain increases in mallard body mass over time. Shorter migration distances would decrease metabolism of energy reserves, potentially resulting in greater body mass (Gunnarsson et al., 2011). In the Northwest European Flyway, mallards experienced an increase in body mass coincident with a shift northward in winter distribution compared to previous decades (Sauter et al., 2010; Gunnarsson et al., 2012). However, Green and Krementz (2008) found no evidence that harvest distributions of mallards had changed in the Mississippi Flyway and concluded there had been no significant, directional changes in the latitude of winter harvest distributions. Likewise, recent mallard harvest data indicate that the number of mallard harvests remains high in the LMAV (Raftovich et al., 2021). While additional data might further refine our understanding of distributional shifts within the LMAV, we do not think the hypothesis that body mass is increasing due to shifts in mallard distributions northward accounts for the body mass changes we documented.

Finally, increases in food availability caused by landscape alteration could potentially be responsible for mallard body mass increase over time. Generally, it is suggested that some waterfowl habitat types have continued to decline in the LMAV over time (LMVJV, 2015). For example, recent studies have shown that bottomland hardwood forests have reduced mast-producing potential due to declining tree health (Nelms et al., 2007; AGFC 2017). Other reports indicate the acreage of crops, such as rice that is utilized by waterfowl, declined in Arkansas and Mississippi at $\leq$ 2.6% annually from 1995 to 2017 (McBride et al., 2018). Crop acreage declines have resulted from technological advancements (e.g., planting earlier maturing crop strains) and management practices (e.g., stripper-header harvesting, fall tillage) that increase farmer yield per acre and require less acreage to be planted (Anders, 2008; McBride et al., 2018). In addition to declines in the area of crops planted, food resources available in fields after harvest have decreased, most notably in rice fields (Stafford et al., 2006). However, scientists and wetland managers have improved the body of knowledge for improving the quality and quantity of waterfowl food resources on the landscapes from 1979 to 2021 (e.g., Fredrickson and Taylor, 2007; Nelms et al., 2007; Hagy and Kaminski, 2012; Williams et al., 2014; Tapp et al., 2018; Behney, 2020). As a result, there should be better food resources per unit area because wetland managers should have a better understanding of what resources are important to waterfowl and how to provide them compared to previous decades. Likewise, in recent years, programs like the Wetland Reserve Program (WRP; now Wetland Reserve Easement [WRE]) have been developed to help restore wetland habitat for waterfowl (Tapp et al., 2018; USDA, 2022). From 1996–2021, 700,000 acres of wetlands have been restored among Arkansas, Mississippi, and Louisiana (USDA, 2021). Although it is unknown whether recent wetland habitat restoration efforts like those seen in WRE programs translate to high quality waterfowl habitat, it is worth noting that these restoration programs could be responsible for increases in mallard body mass from 1979 to 2021.

Detecting long-term increasing trends in body mass is complicated by body mass variation. Although mallards increased in body mass over decades, our results indicated body mass decreased within winters. These results are consistent with several studies that have shown mallard body mass declines from early- and mid-winter to late-winter (e.g., Delnicki and Reinecke, 1986; Whyte et al., 1986; Loesch et al., 1992). In contrast, it is suggested that increases in foraging activity that occur right before spring migration (i.e., hyperphagia) could result in heavier mallards (Bluhm, 1992). However, spring migration typically occurs mid-February through March and our data did not span this period (Dugger, 1997; Krementz et al., 2011). Therefore, slight increases in mass due to hyperphagia are most likely not reflected within our samples. Additionally, research on changes in mallard body mass in captivity show that mallards may continue to decrease in mass despite periods of hyperphagia, even when given an unlimited ad-libitum diet (Pattenden and Boag, 1987; Loesch et al., 1992). Thus, decreases in mallard body mass over winter could be an effort by individuals to reach an optimal (lower) spring departure weight as a migration strategy (Lindström and Alerstam, 1992) or may indicate a decrease in energy reserves needed as a hedge against starvation risk (Reinecke et al., 1982). Alternatively, decreasing body mass may simply reflect decreasing food availability as non-renewing food resources are depleted over winter (Greer et al., 2009).

Our results indicated that variation in the body mass of mallards among years was influenced by climate variables, and the best predictors of mallard body mass were rainfall and river gage height. These variables have often been associated with foraging habitat availability (Delnicki and Reinecke, 1986; Guillemain et al., 2000; Fredrickson and Taylor, 2007). Increased area of surface water from flooding or rainfall increases access to food resources and potentially mallard body mass. Interestingly, river gage height is not correlated with local rainfall, indicating that factors operating upstream or at larger spatial scales complicated relationships between these variables.

We found marginal support for a negative relationship between WSI and mallard body mass. Severe cold weather can decrease access to food resources for dabbling ducks (Schummer et al., 2010) and increase metabolism, which could result in decreased body mass (McKinney and McWilliams, 2005). However, Whyte and Bolen (1984) found that when feeding conditions are optimal, severe cold weather does not affect gains in lipids or body mass. Climate in the LMAV is mild enough during winter that relationships between WSI and mallard body mass probably will be difficult to detect compared to areas with much harsher winter conditions (Pawlina et al., 1993).

While mallard body mass has increased over time and varied within seasons in the LMAV, we can only speculate about potential effects on mallard fitness. Some studies have indicated that increased lipid stores in waterfowl promote survival in both breeding and nonbreeding waterfowl (Heitmeyer and Fredrickson, 1981; Hepp, 1986; Blohm et al., 1987; Reinecke et al., 1988; Dubovsky and Kaminski, 1994; Osnas et al., 2016), as well as benefit reproduction (Krapu, 1981; Heitmeyer, 1988, Dubovsky and Kaminski, 1994). However, other studies indicate that mallards may benefit from lower mass to evade predators (Zimmer et al., 2011). If it is also true that decreases in mass during the winter are an adaptive strategy to avoid starvation or prepare for migration, these decreases in mass could also consequently increase survival and reproductive output in some waterfowl species (Reinecke et al., 1982; Loesch et al., 1992; Lindström and Alerstam, 1992). Our results confirm that waterfowl across disparate flyways are increasing in body mass over time. However, additional targeted research is needed to understand the underlying mechanisms as well as fitness-level consequences for these culturally and ecologically important birds.

Ethics statement

All work was conducted under appropriate institutional animal care and use permits, state permits, and federal permits. For study years 2019–2020 and 2020–2021, we were required to have a state collection permit (permit number 031620201) to age wings of waterfowl at later dates.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data referenced in this article are accessible via GitHub using the following link: https://github.com/jonvon16/Veon_etal_LMAVMallardBodyMassData_1979_2022.git

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Author contributions

K. J. Reinecke formulated hypotheses on which the study originally was based. K. J. Reinecke, D. W. Demarest, and K. M. Hartke collected data during 1979–1983 and 1999–2004. B. C. Dabbert collected data from 1990 to 1991. D. G. Krementz collected data from 2015 to 2017. J. T. Veon collected data from 2019 to 2021, formalized and expanded on K. J. Reinecke's hypotheses, analyzed data, and completed much of the writing. B. A. DeGregorio and D. G. Krementz served as co-supervisors, assisted in developing hypotheses, and contributed substantial edits to the manuscript. L. W. Naylor also assisted in formulating hypotheses and contributed substantial edits to the manuscript throughout its development.

Data depository

The data referenced in this article are accessible via GitHub using the following link: https://github.com/jonvon16/Veon_etal_LMAVMallardBodyMassData_1979_2022.git.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02368.

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