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(*Aix sponsa*)

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Fitness Consequences of Morphological and Behavioral
Variation in Early Life in Wood Ducks (*Aix sponsa*)

By

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THESIS

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Abstract

Individuals within a species or population vary considerably in morphology and behavior. For many species, the specific drivers of variation in these phenotypic traits and their influence on individual fitness are poorly known. In this study, we hatched and reared wood ducks (*Aix sponsa*) in a captive common garden environment and then released them into the wild shortly after fledging age. For each individual, we evaluated metrics of size, growth, and behavior across ontogeny to determine whether individuals vary in morphological and behavioral traits when raised in a controlled captive setting. These individuals (n = 106 females) were then released into wild study populations where we tracked first year survival and multiple longer-term measures of fitness through standard monitoring methods and radio frequency identification. Using multivariate statistics and generalized linear models, we analyzed early life variation in morphology and behavior and their influence on individual fitness. Despite identical rearing conditions, we found considerable inter-individual variation in both morphological and behavioral traits. Additionally, we found correlations among egg size, hatch size, and fledging size, although maximum growth rate was the strongest predictor of fledging size. Contrary to evidence in the literature, we found no indication that morphological traits had any influence on first year survival; however, there was some evidence that survival was positively influenced by tonic alertness. We found evidence that both morphology and behavior were influential in multiple measures of long-term success. Here, our strongest results showed a negative relationship between initial size and longevity, and a positive relationship between tonic alertness and number of years incubating. The results of this study shed new light on the development of phenotypic variation in precocial birds and its consequences for individual fitness, and provides insight for captive breeding programs and conservation efforts.

Introduction

The existence of variation among individuals within the same species or populations is well documented (Bolnick et al., 2003, 2011; Kendall & Fox, 2002; A. J. Wilson & Nussey, 2010). However, for many species across multiple taxa, the relative importance of specific factors that drive inter-individual variation and their influence on individual fitness are poorly known. According to the pace-of-life syndrome hypothesis, individual variation can encompass consistent covariation in a broad suite of traits that includes size, morphology, growth rate, and behavior (Montiglio et al., 2018; Réale et al., 2010; Ricklefs & Wikelski, 2002). These traits often fall along a fast-slow life history continuum leading to distinct differences in individual life trajectories. Accordingly, variation in conditions that select for the development of certain individual traits may affect the development of other traits leading to distinct phenotypic variation that encompasses multiple aspects of an individual's physiology, morphology, and behavior (Monaghan, 2008; Montiglio et al., 2018; Réale et al., 2010; Ricklefs & Wikelski, 2002; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, et al., 2004).

Conditions that influence phenotypic variation among individuals typically include some combination of genetics, maternal effects, and early life environment, all of which can have lifelong fitness consequences (Monaghan, 2008; Mousseau & Fox, 1998). The importance of genetics in phenotypic determination is relatively well established (Boake et al., 2002). However, the early life period and its relationship to the development of phenotypic variation is less understood in many species (Eyck et al., 2019; Mueller, 2018; Murren, 2012). Hence, careful evaluation of the ontogenetic period (i.e., all early life developmental events during the life of an organism) is necessary to identify factors that most influence the shaping of individual variation. However, previous studies investigating these dynamics have tended to be narrowly focused and

conducted primarily on captive organisms. In this study, we used a novel approach to investigate the influence of the ontogenetic period on future fitness in a species of wild bird. First, we evaluated morphological and behavioral development in multiple traits across ontogeny in a captive common garden setting. We then followed the same individuals after releasing them into the wild to examine the influence of ontogeny and early morphological and behavioral development on first year survival and longer-term measures of fitness in a natural environment.

Phenotypes are determined by multiple influences; thus it is reasonable to assume that phenotypic variation stems from variation in one or more determining factors. Maternal effects particularly can substantially influence offspring traits including the conferral of early life advantages in initial size and growth rate (Bernardo, 1996; Mousseau & Fox, 1998). According to the silver spoon hypothesis (Minias et al., 2015; Monaghan, 2008; Pigeon et al., 2017; Song et al., 2019; van de Pol et al., 2006), individuals that begin life with early advantages in size and condition are likely to maintain them throughout life, leading to higher lifetime fitness and success than individuals with lower initial quality. This means that initial maternal investment may be critical for the lifetime success of their offspring. In addition to maternal effects, ecological and environmental pressures encountered during ontogeny – such as food availability (Mikolajewski et al., 2005; Pérez et al., 2016; Segers & Taborsky, 2011), predation risk (S. L. Ball & Baker, 1996; Beckerman et al., 2007; Benard, 2004; Peacor et al., 2020), and temperature, both during incubation (Booth, 2006; Durant et al., 2013; Noble et al., 2018) and during offspring development (McCarty & Winkler, 1999; Monaghan, 2008; O’Dea et al., 2019) – may all be important contributors to phenotypic variation.

The influence of early life conditions on morphological and behavioral traits leading to distinct phenotypes is widely acknowledged (Sih, Bell, & Johnson, 2004; Stamps, 1991; D. S.

Wilson, 1998). However, because of the challenges associated with studying organisms in the wild, research examining long-term consequences of phenotypic development is relatively uncommon in free-living animals, especially birds (Moiron et al., 2020; Réale et al., 2007). Robust assessment of morphological and behavioral development with repeated measures taken across ontogeny is difficult and invasive, if not impossible, to conduct in the wild. Consequently, we have incomplete understanding of how and why some traits develop during ontogeny and what the short- term and long-term consequences are with relation to phenotype, survival, longevity, and reproductive success.

In waterfowl, initial offspring size appears to be critical; multiple studies indicate that larger eggs result in larger offspring and that larger versus smaller offspring generally have higher rates of survival, recruitment, and reproductive success (Anderson & Alisauskas, 2001; Dawson & Clark, 1996, 2000; Pelayo & Clark, 2002, 2003; B. S. Sedinger et al., 2018; J. S. Sedinger et al., 1995; J. S. Sedinger & Chelgren, 2007). Furthermore, shortly after hatching, most neonate waterfowl face intense predation and the possibility of starvation leading to high mortality rates in the first 1-3 weeks of life (Batt, 1992). Thus, pre-hatch maternal investment in eggs and initial offspring size appears to be critical in providing offspring with early life advantages. However, while existing evidence indicates that offspring size is important, most studies of survival and reproductive success in waterfowl typically evaluate the influence of an individual's size at only a single point in time. Examination of morphological traits and their development across ontogeny has not been studied robustly in relation to survival and longer-term measures of fitness. For example, there has been very little investigation into the relationship between early growth rate and longevity. The long-term influences of ontogenetic behavioral development have received even less attention. Again, these factors lead to an

incomplete understanding of the relationships between early life development in morphological and behavioral traits and their longer-term influence on survival and lifetime measures of success.

In this study, we examine the ontogenetic period of a precocial bird to assess its importance in the development of morphological and behavioral traits and to evaluate the longer-term consequences of these traits for survival and future reproductive success. To explore these relationships, we studied wood ducks (*Aix sponsa*) that were hatched and reared in a controlled captive setting and later released into the wild. Wood ducks are an ideal species for studying morphological and behavioral trait development because their precocial offspring are completely mobile and independent in terms of movement and self-feeding within 24-48 hours of hatching (Hepp & Bellrose, 2013). This allows for robust evaluation of the development of multiple traits across ontogeny, including assessment of both individual behaviors and growth rates during life stages that are particularly important yet rarely studied in precocial birds.

Wood ducks also exhibit conspecific brood parasitism (Semel et al., 1988; Semel & Sherman, 1986, 2001a), where, as an alternative or in addition to incubating their own eggs, some females lay eggs in the nests of other wood ducks. This behavioral variation in reproductive strategy makes wood ducks a particularly interesting system in which to examine the development of behavioral and morphological variation. Variation in adult reproductive strategy may be influenced by early life development or experiences. Unlike most birds, wood duck females are extremely philopatric in the wild (Bellrose & Holm, 1994; Hepp et al., 1987, 1989; Hepp & Kennamer, 1992; Semel & Sherman, 2001b) which allows us to track released, individual females from hatching through their reproductive lifespans, facilitating direct evaluation of multiple measures of individual lifetime fitness in relation to phenotypic traits.

Thus, this study is unique in that we were able to assess individual phenotypic trait development in a controlled captive setting, and then evaluate the long-term fitness consequences of those traits by following the same individuals in the wild, post release.

Such analyses are interesting not only from a behavioral ecological perspective, but also have relevance to conservation programs. It is common practice to raise species of conservation concern in captivity with the aim of releasing those individuals into the wild at some point after rearing. There is now a growing body of literature on the importance of considering behavioral and social dynamics of the individuals and populations to be released (Johnsson et al., 2014; Kreger et al., 2004; Shier & Owings, 2007), but often we have little knowledge or analysis of how early life experiences or maternal effects during development might influence survival and reproductive success post release. To our knowledge, few other studies have attempted to study this.

We had two primary objectives in this study. The first was to explore early life morphological patterns and relationships in this precocial bird. The second objective was to investigate the influence of early life development in morphology and behavior on first year survival and longer-term measures of fitness.

For our first objective, we examined patterns of variation among individuals in morphological size and growth in a common garden experiment. Here we tested simple pairwise relationships among egg size, hatch size, growth rate, and fledging size to understand how initial size and growth rate influence fledging size when individuals are raised in a common garden. We then examined covariation of morphological traits among individuals to better understand relationships between size and growth rate. One possible outcome of this evaluation is that initial morphological size predicts size later in life (i.e., egg size, hatch size, and fledging size are all

correlated). Similar patterns have been observed in wild wood ducks (Eadie, Wells et al., unpublished data) and in other species of waterfowl (Cooch et al., 1991; Dawson & Clark, 1996; B. S. Sedinger et al., 2018; J. S. Sedinger et al., 1995; J. S. Sedinger & Chelgren, 2007). A second possible outcome is that we find little or no relationship among these measures of size when individuals are raised in a common garden where environmental conditions are benign and standardized (i.e., previous or current size does not predict future size).

For our second objective, we tested the hypothesis that early life morphology and behavior would be related to first year survival and longer-term measures of fitness. We predicted that egg and duckling size would be positively related to survival, longevity, and reproductive success, as has been suggested for other species of waterfowl (in effect, the silver spoon hypothesis; Dawson & Clark, 1996, 2000; Pelayo & Clark, 2002; B. S. Sedinger et al., 2018; J. S. Sedinger et al., 1995; J. S. Sedinger & Chelgren, 2007). An alternative prediction is that size would be negatively related to survival, longevity, and reproductive success if there are costs to fast growth and larger size which make smaller individuals more successful long-term (see Mangel & Stamps, 2001; Monaghan, 2008; Rotella et al., 2003). It is more difficult to predict a directional relationship between behavior and measures of fitness. Here, we examine variation in behaviors related to space use and intensity of response to stimuli (see methods). In both cases, optimal behavior can depend heavily on environmental conditions such as predation risk and food abundance (Brown, 1999; Lima & Dill, 1990; Mangel & Stamps, 2001). Accordingly, there may be either a positive or negative relationship between behavioral measures and survival, longevity, and reproductive success. To evaluate behavioral variation, multiple assays were conducted for each individual. Assays were designed to assess individual variation in space use and response to threatening stimuli (simulated predator threat). We used

multivariate statistical analyses to examine relationships among behaviors across all assays. We then examined the relative influence of morphological versus behavioral traits on survival, longevity, and multiple measures of reproductive success.

Methods

Egg Collection and Incubation

We collected viable unhatched wood duck eggs from both active and inactive (abandoned or depredated) nests at four long-term study sites in the Central Valley of California. Most of our eggs were collected from nests that had been abandoned or were never incubated. We recognize that viability or quality of eggs may not fully represent all eggs in the population, however, collecting eggs exclusively from active nests would have impacted our on-going long-term studies of reproductive ecology in our wild populations.

All eggs were collected, and all ducklings were reared under scientific collection permits from the U.S. Fish & Wildlife Service (MB230246, MB73393B, MB789345) and the California Department of Fish and Wildlife (SC-009565). All banding was conducted under a master banding permit to JME from the Bird Banding Lab, USGS (10562) and all field work, captive-rearing, and behavioral studies were approved by UC Davis Institutional Animal Use and Care Committee (Protocols #17535, 20971, 22236, 22698). Our study sites consisted of 16-200 wood duck nest boxes maintained annually by field teams and property owners. Nest boxes were monitored for active use by wood ducks both through regular manual checks and through radio-frequency identification (RFID). All female wood ducks in our study populations were equipped with a unique passive integrated transponder (PIT) tag which is recorded by an RFID unit

attached to each nest box. Each nest box visit by a tagged female was recorded by the RFID unit (see description in Bridge et al., 2019).

Unhatched eggs were transported within 1-3 hours to our onsite vivarium at the University of California Davis and moved into humidity and temperature-controlled incubators until they either hatched or ceased to develop, a span of approximately 30 days. Incubation conditions were maintained at approximately 35.9 degrees Celsius and 60-80% humidity from incubation onset through hatching (Durant et al., 2013). All eggs were given daily incubation breaks to mimic natural conditions, as female wood duck may take two incubation breaks per day (Manlove & Hepp, 2000). Eggs were monitored daily during the incubation period by egg candling to assess embryonic development (Weller, 1956).

Aviary

Ducklings were housed in captivity in broods of 5-10 individuals of similar age. Housing enclosures were three-by-six meters consisting primarily of wood and hardware cloth. Enclosure bottoms were concrete covered with approximately ¼-inch of soil. Each enclosure also contained at least one box to provide ducklings with refuge. Wooden perches were also provided in each enclosure. A circular pool (1.5 meters in diameter) with approximately 15cm of water was added to each enclosure after the first week. Ducklings were raised in a common garden and provided food and water *ad libitum*.

Growth and Morphometric Measurements

Upon hatching, each individual duckling was marked with a unique PIT tag, injected subcutaneously between the scapulars for subsequent identification. Blood samples were

collected from each individual for genetic analysis to assign maternity. Morphometric measurements were obtained for body mass and tarsus length immediately upon hatching and at minimum once every week following hatching for at least the first five weeks of life in order to generate individual growth rate curves. In wood ducks, week 5 is the age at which most hard tissue growth is complete and the approximate age of fledging or abandonment by the mother (Ball et al., 1975; Beard, 1964; Hinton, 2022). Instantaneous growth rates of body mass and tarsus length were estimated for each individual by calculating the slope of the tangent line for every discrete measurement in each growth curve (Hinton, 2022).

Open Field Behavioral Tests

We used data from a larger study conducted by Hinton (2022). Briefly, a series of open field tests (OFTs) were conducted to evaluate early life behavioral responses to novel environments and stimuli. The OFTs were conducted bi-weekly at ages one, three, and five weeks, for a total of three tests per individual. The tests were administered in a behavioral arena with four walls and water covering a grid patterned floor (Figure 1). The arena also contained various artificial plants. Ducklings began the test in an acclimation chamber for several minutes. After this period, a door was opened and ducklings were free to leave the chamber on their own. After 7 minutes, the chamber was removed regardless of whether or not the ducklings had emerged. Ducklings were then given 5 minutes after the removal of the acclimation chamber to move around and explore the arena. The following five behavioral metrics were scored: (1) total number of grid lines crossed over the duration of the test (activity); (2) intensity of response to the removal of the acclimation chamber scored on a scale of 0-5 (startle response); (3) intensity of response to the observer removing the duckling from the arena at the conclusion of the test

scored on a scale of 0-5 (response to observer); (4) proportion of time spent in grid squares that were not adjacent to walls (anti-thigmotaxis); and (5) proportion of time spent near the location of the acclimation chamber, post removal (startle stimulus revisitation). We used the behavioral scores obtained from the OFTs to evaluate individual variation in behavioral responses. We assumed that both stimuli (acclimation chamber removal and interaction with the observer) would be perceived as potential predator threats. As such, subsequent intensity of response to both stimuli and level of activity afterward were interpreted as how individual birds might respond in the presence of a predator. When a duckling avoided the site of the acclimation chamber area post removal and remained close to the walls rather than moving freely about the arena, we rationalized that this too was a “predator response” behavior. What we wanted to assess was the potential individual variation in these behaviors and their influence, if any, on measures of individual fitness.

In-Hand Behavioral Tests

To evaluate early life behavioral responses to handling, we performed a series of tonic immobility and tube struggle tests (Hinton, 2022). Both tests were conducted on each individual shortly after hatching and once every week afterward until at least 5 weeks of age. Here, we assumed that these tests functioned as measures of how individuals would respond had they been captured by a predator. Tonic immobility has been described in the literature as a post-capture anti-predator behavioral response (Humphreys & Ruxton, 2018; Sargeant & Eberhardt, 1975). To test for individual variation in tonic response, we conducted a simple tonic immobility test (see Hinton, 2022). For the test, a maximum of five attempts were made to induce tonic immobility. We were not able to induce a state of immobility in every individual. For each test

we recorded the number of attempts necessary to induce tonic immobility (tonic attempts), the alertness of each individual while in a tonic state scored from 1-3 (tonic alertness), and the duration they remained tonic and immobile, up to 60 seconds (tonic duration). Struggle tests were used specifically to evaluate individual responses to being physically “trapped” or “restrained.” To perform the struggle test, each duckling was placed head down in a small, opaque tube. For 30 seconds, we recorded the total number of struggle attempts initiated (i.e., a struggle test).

Release Study Sites

After completing the morphological and behavioral assessments, we released 106 captive-reared female wood ducks into three wild study populations located on private and public ranches in the Central Valley of California. Distances between these study sites ranged from 18-30 kilometers. Each individual was fitted with a USGS aluminum leg band. Morphometric measurements were repeated just before release. We verified the presence of a PIT tag in each duck prior to its release. Utilizing both RFID technology and on nest captures during incubation, we tracked individual females post release every breeding season until they were no longer detected by either method. Female wood ducks exhibit strong natal philopatry (Hepp et al., 1987, 1989; Hepp & Kennamer, 1992; Semel & Sherman, 2001b) and most individuals prospect for nesting sites, lay eggs parasitically, and/or incubate their own nests each year (Semel et al., 1988; Semel & Sherman, 1986, 2001a), all of which are detected by one or both of the methods described above. Therefore, we are confident that we detected all PIT tagged females that were alive and present in our study populations during the breeding season.

All nest boxes and active nests in our study populations were monitored through regular nest checks. For every nest box, we tracked the number of eggs laid and the number of ducklings that hatched and exited a nest. Every duckling that hatched in our study populations was measured and fitted with its own unique PIT tag. We also collected a blood sample for parentage analysis using 18 microsatellite DNA markers to assign maternity to each duckling using program Colony (see Thow, 2019 and Thow et al., 2022 for description of methods and validation of parentage assignments). These techniques enabled us to estimate the total number of ducklings produced by each female in our study regardless of reproductive strategy (nesting or parasitism).

Statistical Analysis: Early Life Patterns of Morphological Growth and Development

To evaluate the morphological relationships between early life size and size at fledging age (5 weeks), we conducted a series of linear regression analyses testing pairwise relationships among egg size, hatch size of mass and tarsus, maximum growth rates of mass and tarsus, and week 5 size of mass and tarsus to evaluate the best predictors of duckling size at week 5. We then used principal components analysis (PCA) to (a) further examine the relationships and covariation between early life growth and morphological traits and (b) reduce correlated variables to uncorrelated principal components to account for multicollinearity while maintaining as much information as possible for use in subsequent analyses. Variables that were included in our PCA were: egg mass, hatch mass, hatch tarsus length, maximum growth rate of mass, and maximum growth rate of tarsus length. We used linear regression models in R version 4.1.3 (R Core Team, 2022). The PCA was conducted using JMP[®], Version 16 (SAS Institute Inc., Cary, NC, 1989–2021).

Statistical Analysis: Influence of Early Life Morphology and Behavior on Future Success

To evaluate patterns of early life behavior in wood ducks, we reanalyzed data from Hinton (2022). In their study, Hinton (2022) analyzed data from two cohorts (2016 and 2017) separately. In this study, we combined data from 2016 and 2017 into a single group for a larger sample size and greater statistical power in our analyses. We used eigen decomposition to evaluate relationships among behaviors measured across ontogeny. Because our dataset included repeated behavioral measures, we used eigen decomposition rather than PCA to address pseudoreplication and ensure accuracy in our analyses (see discussion in Hinton, 2022). Eigen decomposition performs similarly to PCA but is preferred for repeated measures data obtained from the same individuals (Hinton, 2022). We conducted two separate analyses of behavioral data: (1) behaviors measured during open field tests: startle stimulus revisitation, anti-thigmotaxis, activity, startle response, and response to observer; and (2) behaviors measured during in-hand tests: tonic alertness, tonic attempts, tonic duration, and struggle test. The principal component (PC) scores obtained from both eigen decomposition analyses were used in subsequent behavioral analyses. Eigen decomposition analyses were conducted using R version 4.1.3 (brms package, Bürkner, 2017; RStan package, Stan Development Team, 2023; R Core Team, 2022).

To investigate the influence of specific morphological traits individually on post-release survival to adulthood, we conducted seven different single variable binomial generalized linear models. The predictor variables for these models included: egg size, hatch mass, hatch tarsus length, week 5 mass, week 5 tarsus length, maximum growth rate of mass, and maximum growth rate of tarsus length. To investigate the influence of specific behavioral traits individually on post-release survival to adulthood, we used a second set of nine different single variable

binomial generalized linear models. The predictor variables for these models included: tonic attempts, tonic alertness, tonic duration, struggle test, startle response, response to observer, anti-thigmotaxis, startle stimulus revisitation, and activity.

To evaluate the influence of early life morphology and behavior on post-release survival and longer-term success, we examined specific measures of success in three categories: apparent survival to adulthood (usually detection occurred the first year after release, however, five surviving individuals were not detected until the second year after release) and longevity; reproductive strategy; reproductive investment and success. These metrics were only assessed for females because males disperse while females are highly philopatric. Apparent survival to adulthood was modeled as a simple binary variable, scored as 1 for any bird that was detected in the population the first time after release (usually in their first year), and 0 for all others. Females may have emigrated from the study area and so we refer to this only as apparent survival. We included all 106 released wood duck females in this analysis. To evaluate longevity, we modeled the total number of years that each individual was detected in our wild study populations, once they had recruited to the population. Here, we analyzed only the individuals that survived after release and were detected at least once in the wild, post release. To evaluate reproductive strategy, we modeled both the number of years that each individual incubated a nest and the proportion of total nest boxes that each individual visited per year. For these analyses, we included only the surviving individuals. In our evaluation of reproductive investment and success, we modeled average clutch size for each individual that incubated a nest, number of years in which each individual successfully hatched a nest, and the total number of ducklings produced by each individual (through both nesting and parasitism). For these analyses, we also included only the surviving individuals.

For all analyses, we built a candidate model set of four generalized linear models. The full model included the predictor variables: PC1 Initial Size, PC2 Growth Rate, PC1 Response Intensity, PC2 Space Use, PC1 Tonic Alertness, and PC2 Struggle Intensity. We also generated three reduced models that included (1) morphological variables only (PC1 Initial Size and PC2 Growth Rate); (2) behavioral variables only (PC1 Response Intensity, PC2 Space Use, PC1 Tonic Alertness, and PC2 Struggle Intensity); and (3) intercept only. The PC scores were obtained from our PCAs and eigen decomposition analyses. We included PC scores rather than raw morphological and behavioral scores to account for problems associated with multicollinearity. We used binomial generalized linear models to model survival and we used gaussian generalized linear models for all other response variables (Fisher, 1928).

For all models, parameter estimates and confidence intervals were back transformed after analysis, where applicable, to simplify interpretation. We used Akaike Information Criterion (AIC) values to rank models in each candidate model set. We used cumulative AIC weights to determine the relative weight of each variable in our candidate model sets. In our analyses of apparent survival to adulthood, we used our full dataset that included every released female ($n = 106$). For all other analyses evaluating post survival measures of success, we used a subset of the full dataset that included only individuals confirmed to have survived to adulthood and to be alive in our study population post release ($n = 33$). We used the reduced dataset to address extreme skew and bias due to zero inflation resulting from the 73 individuals that did not survive post release. All linear regression models were performed using R version 4.1.3 (R Core Team, 2022).

Results

Early Life Patterns of Morphological Growth and Development

Within our study population of captive-reared female wood ducks, we found substantial variation in size and growth rate among individuals despite identical rearing conditions (Figure 2). The range of variation was somewhat surprising: sizes of newly hatched ducklings ranged from 19-34 grams, growth rates for mass ranged from 8 to 18 grams/day and by week 5, mass of ducklings ranged from 218-463 grams. This was unexpected given that all ducklings had equal and unlimited access to food and were free from any influences of predation risk or extreme weather conditions, yet size and growth rates varied 2-3-fold among individuals.

Our results suggest that some of this variation can be attributed to initial maternal investment. Larger eggs produced larger ducklings; linear regression analysis revealed a significant relationship between egg mass and hatch mass ($R^2 = 0.55$, $P < 2e-16$; Figure 3). Similarly, there was a significant relationship between egg mass and hatch tarsus length ($R^2 = 0.34$, $P = 4.9e-10$). Interestingly, there was no effect of egg size on either maximum growth rate of mass ($R^2 = -0.002$, $P = 0.37$) or maximum growth rate of tarsus ($R^2 = -0.003$, $P = 0.38$). There was also no effect of hatch size of mass or tarsus on maximum growth rate of either mass ($R^2 = -0.01$, $P = 0.77$) or tarsus ($R^2 = -0.01$, $P = 0.1$), respectively. Accordingly, size and growth rates appear to be somewhat independent.

Egg size, hatch size, and maximum growth rates were all significantly related to fledging size (week 5). There were significant relationships between hatch mass and week 5 mass ($R^2 = 0.05$, $P = 0.01$; Figure 4), and between maximum growth rate of mass and week 5 mass ($R^2 = 0.70$, $P < 2e-16$; Figure 5). Likewise, there were significant relationships between hatch tarsus

length and week 5 tarsus length ($R^2 = 0.24$, $P < 0.001$), and between maximum growth rate of the tarsus and week 5 tarsus length ($R^2 = 0.29$, $P < 0.001$).

Principal components analysis (PCA) helped to further clarify the relationships among these early life morphological traits. Egg mass, hatch mass, and hatch tarsus length loaded strongly on PC1 while maximum growth rate of mass and tarsus length loaded strongly on PC2 (Table 1). This analysis indicates that morphological traits can effectively be partitioned along two independent dimensions, one reflecting overall size (PC1) and a second representing growth rates (PC2). An individual with a high PC1 score is larger overall than an individual with a low score. Likewise, an individual with a high PC2 score has a higher growth rate than an individual with a low score. Although we would expect these to be correlated, PCA analysis suggests that they represent statistically independent processes influencing duckling and fledgling morphology (we henceforth refer to these as *PC1 Initial Size* and *PC2 Growth Rate*). Together PC1 and PC2 explained 76.5% of the variance in the data. In subsequent analyses, we used PC scores from this analysis as predictor variables to account for multicollinearity while still maintaining as much information as possible from the original morphological variables of interest.

Early Life Patterns of Behavioral Variation

For our analyses of behavioral relationships, we used eigen decomposition to evaluate within individual covariation in behavioral traits. The results of these analyses confirmed the findings of Hinton (2022) that behaviors measured during ontogeny do covary at the individual level.

Analyses of open field tests indicated that post-stimulus activity level, startle response, and response to the observer all loaded positively on PC1, while startle stimulus revisitation and

anti-thigmotaxis loaded positively on PC2 (Table 2). All three behaviors that loaded on PC1 measure some aspect of intensity of response to a stimulus, whereas both behaviors that loaded on PC2 measured how individuals move around their environment. Here, an individual with a high PC1 score responds more strongly overall to stimuli than an individual with a low score while an individual with a high PC2 score explores a larger area of its environment than an individual with a low score. These results suggest that there are two independent axes of behavioral variation in open field tests – PC1 reflects overall response intensity while PC2 reflects space use (accordingly, we refer to these as *PC1 Response Intensity* and *PC2 Space Use*.)

In analyses of in-hand tests, tonic alertness, tonic attempts, and tonic duration all loaded strongly on PC1, while struggle test scores loaded strongly on PC2 (Table 2). An individual with a high PC1 score displays lower overall intensity of tonic immobility (i.e., is less likely to enter a tonic state, remains tonic for a shorter duration, and is more alert while in a tonic state) than an individual with a low score. An individual with a high PC2 score struggles more overall than an individual with a low score. Here, PC1 measures susceptibility to tonic immobility and overall tonic alertness while PC2 directly measures struggle intensity (we refer to these as *PC1 Tonic Alertness* and *PC2 Struggle Intensity*, respectively).

Our analyses revealed considerable variation in behavioral measures among individuals (Figure 6). Results of the open-field tests (panels A and B, Figure 6) suggest a skewed distribution with a smaller number of individuals exhibiting more extreme *response intensity* and *space use* (right hand tail). Skew was less pronounced in measures of in-hand behaviors (Figure 6, C and D) although *struggle intensity* (PC2, panel D) appeared bimodal, suggesting stronger, more dimorphic differences among behavioral types. Separate analyses by Hinton (2022) showed

that individual ducklings are consistent in their behavioral responses over the entire growth period with significant repeatability (measured as the intraclass correlation coefficient) across ontogeny and even into adulthood. Our results relating to covariation confirm those of Hinton (2022), where individual cohorts were analyzed separately, in demonstrating that ducklings reared in captivity in a common garden experiment exhibit consistent behavioral variation throughout their early life.

Influence of Early Life Morphology and Behavior on Future Success

Of the 106 female wood ducks released into our wild study populations, 33 (31%) were detected alive during a future time period. We confirmed that birds had returned to the study area both by capturing females on a nest and by recording a female's presence via RFID reads of her unique PIT tag. The novelty of this approach is that we could determine that a female had survived and returned (and visited at least one nest) even if she was never caught or seen.

Examination of our seven different morphological traits using single variable models revealed no significant effect of morphological size or growth rates on *apparent survival to adulthood* (binary trait) (Table 3). Similarly, we examined nine different behavioral measures in single variable models. Here, only *tonic alertness* was related to *apparent survival* ($P = 0.04$, slope estimate = 0.686; Figure 7; Table 4).

The results of our multi-variable analyses, however, indicated that *apparent survival to adulthood* and *number of years detected* in our study populations (longevity) were influenced by both morphology and behavior. The top model in our candidate model set examining apparent survival to adulthood was the full model (Table 5). The variables *space use* (0.868) and *response intensity* (0.778) had the greatest model weights (range 0.44-0.868) influencing the two

variables, survival and years detected (Table 5). The second ranked model which included only the four behavioral variables was numerically equivalent to the top model in terms of AIC ($\Delta\text{AIC} = 1.42$). Both the full model and the behavior-only model ($\Delta\text{AIC} = 1.42$) had much greater support than either the morphology-only ($\Delta\text{AIC} = 12.60$) or the intercept-only ($\Delta\text{AIC} = 35.54$) model. Our assessment of cumulative AIC weight for each variable indicated that *PC2 Space Use* and *PC1 Response Intensity* were the most strongly weighted variables, respectively. The four behavioral variables each had greater weights than the morphological variables, although no individual variable appeared to be significant on its own (Table 5).

In multi-variable analyses of the *number of years that individuals were detected* (longevity), the full model was again the top model in our model set (Table 5). The behavior-only model was numerically equivalent to the top model ($\Delta\text{AIC} = 1.24$; Table 5); however, the R^2 value for the behavior-only model was lower meaning that the full model explained a higher proportion of the variance.

Cumulative AIC weights indicated that *PC2 Space Use* (0.538) and *PC1 Response Intensity* (0.515) were the most strongly weighted variables among all variables (range 0.140-0.538). In the full model, we also found evidence that morphology predicted the *number of years detected* in our study populations. As *PC1 Initial Size* increased, the *number of years detected* decreased (slope estimate = -0.31, 95% CI [-0.62, -0.01]; Figure 8; Table 5). *PC1 Initial Size* was the only variable in the model with a confidence interval that did not overlap zero.

Our analyses of reproductive strategy provided evidence that both morphology and behavior influenced the *number of years that individuals incubate nests*. The top model in our candidate model set was the full model (Table 6). The behavior-only model was numerically equivalent to the top model ($\Delta\text{AIC} = 1.06$). Both models had moderately large R^2 values (0.54

and 0.42, respectively). Again, weights of all behavioral variables (range = 0.939-0.980) were stronger than the morphological variables (range = 0.591-0.592; Table 6). The full model indicated that *PC1 Tonic Alertness*, *PC1 Response Intensity*, and *PC2 Space use* were all predictive of *number of years incubating*. As *PC1 Tonic Alertness* increased, *number of years incubating* increased (slope estimate = 0.54, 95% CI [0.20, 0.87]; Figure 9; Table 6). As *PC2 Space Use* increased, *number of years incubating* also increased (slope estimate = -0.52, 95% CI [0.10, 0.93]; Table 6). However, as *PC1 Response Intensity* increased, *number of years incubating* decreased (slope estimate = -0.43, 95% CI [-0.82, -0.04]; Table 6).

The top model in our candidate model set examining the *proportion of total nest boxes that individuals visited* was the intercept only model (Table 6). Models including morphology only ($\Delta\text{AIC} = 18.76$) and behavior only ($\Delta\text{AIC} = 24.25$) received much less support. Cumulative AIC weights for all morphological and behavioral variables were zero, indicating that morphology and behavior had no effect on nest box visitation rates.

Our analyses of reproductive investment and success provided some evidence that both morphology and behavior were influential. The top model in our candidate model set examining *average clutch size* was the behavior-only model (Table 7). The second ranked model was the full model which was numerically equivalent to the top model ($\Delta\text{AIC} = 0.48$). However, the full model explained a higher proportion of the variance (R^2 values, 0.37 vs. 0.21). The most strongly weighted variable by cumulative AIC weight was *PC1 Response Intensity* (0.707); the next most strongly weighted variable was *PC2 space use* (0.366).

The top model in our candidate model set examining the *total number of successful nesting years per individual* was the full model ($R^2 = 0.58$, Table 7). Cumulative AIC weights showed that all behavioral variables (range = 0.532-0.802) were more strongly weighted than the

morphological variables (range = 0.442-0.456). *PCI Response Intensity* was the most important variable and was found to predict *number of successful nesting years* (slope estimate = -0.56, 95% CI [-1.02, -0.09]; Table 7).

The top model in our candidate model set examining *number of ducklings produced* was the behavior-only model (Table 7). The full model was numerically equivalent to the top model in terms of AIC ($\Delta\text{AIC} = 1.53$) and explained more variance in terms of R^2 value (0.21 vs.0.12). Again, *PCI Response Intensity* was by far the most strongly weighted variable (0.772). Weights of all other variables in this category ranged from 0.023-0.298. However, confidence intervals for all variables in this category overlapped zero in both of the top models, indicating poor predictive power.

Discussion

We found considerable morphological variation among individual females in hatch size, growth rate, and size at week 5 in our study population of captive wood ducks. Growth rate and week 5 (fledging) size varied among individuals despite identical rearing conditions. For morphological relationships, we found that egg size predicted hatch size and hatch size predicted fledging size, though the second relationship was weaker than the first. Interestingly, maximum growth rate was a stronger predictor of fledging size than hatch size, although both were influential. Overall, we found strong covariation in measurements of initial size (egg mass, hatch mass, hatch tarsus length) and in maximum growth rates of mass and tarsus length. Our analyses also revealed covariations among behavioral traits measured in both open field and in-hand tests. Our combined-cohort analysis of wood ducks from Hinton's (2022) dataset reaffirmed behavioral relationships found in that study. In our study, we were surprised to find no evidence

that survival to adulthood was related to any single measure of morphological size or growth, however, we did find some evidence that behavior was influential. In captive-reared wood ducks, early life development in morphology and behavior appeared to be most consequential for fitness only after individuals survive to adulthood. Here, we found evidence suggesting that both morphology and behavior influenced longer-term fitness, however, behavior was found to be more influential in most cases and appeared to have some influence on nearly every measure of fitness we examined.

Early Life Patterns of Morphological Growth and Development

Prior studies in wood ducks and other waterfowl species have demonstrated that egg size predicts hatch size and hatch size in turn predicts adult size (Anderson & Alisauskas, 2001; Dawson & Clark, 1996, 2000; Pelayo & Clark, 2002, 2003; B. S. Sedinger et al., 2018; J. S. Sedinger et al., 1995; J. S. Sedinger & Chelgren, 2007). We previously observed similar relationships in our wild wood duck study populations in California (Eadie, Wells et al., unpublished data). In this study we found that these patterns generally held true for wood ducks even when hatched and reared in a common garden environment with surplus food and no predators or perceived environmental stress. However, our study differed notably from previous studies in that we were able to track variation in growth rates throughout the entire growth period to examine covariation among early life morphological traits through fledging age. Studies investigating morphological patterns in wild, free-living waterfowl have rarely measured either growth rate or size at fledging. Our captive-rearing environment provided novel findings regarding potentially important and understudied measures of early life variation.

Maximum growth rate was the strongest predictor of fledging size for captive-reared wood ducks in our study. Cooch (2002) found a similar relationship in snow geese, but hatch date also was influential. In our study, egg size and hatch size also influenced fledging size, but these relationships were weaker than maximum growth rate. Interestingly, maximum growth rates were unrelated to either egg size or hatch size in our study. Principal components analysis (PCA) confirmed these relationships (Table 1) by verifying that egg mass, hatch mass, and hatch tarsus length all covaried along the first axis of variation (PC1) while maximum growth rates of mass and tarsus length covaried along the second axis of variation (PC2).

Our findings of the effects of maximum growth rate diverge somewhat from the waterfowl literature where evidence suggests that larger offspring generally tend to both grow faster and become larger adults (Cooch, 2002; Dawson & Clark, 2000; B. S. Sedinger et al., 2018; J. S. Sedinger et al., 1995; J. S. Sedinger & Chelgren, 2007). Perhaps one explanation for our this is the absence of selective pressures in the captive-rearing environment. Ducklings raised in captivity face no risk of predation or starvation during the early life period where these pressures often lead to high rates of mortality in the wild. With selective pressures on free-living birds, offspring of larger initial size may have a distinct advantage in both food acquisition and predator evasion (Brown, 1999; Claessen et al., 2002; Lima & Dill, 1990; Mangel & Stamps, 2001). However, the availability of food *ad libitum* with no risk of predation appears to allow smaller individuals to compensate somewhat for their initial disadvantage in size by growing at a faster rate, a scenario likely facilitated through safe and easy access to food in captivity. If correct, this explanation supports our finding that maximum growth rate, not hatch size, was the strongest predictor of fledging size.

Influence of Early Life Morphology and Behavior on Future Success

Our confirmation of behavioral covariation in wood ducks supports the findings in Hinton (2022). Collectively, behaviors that were measured during the open field tests have been interpreted to represent pre-capture predator avoidance strategies (Hinton, 2022). Measures of *response intensity* are consistent with fleeing versus hiding, whereas measures of *space use* are consistent with risk acceptance related to movement and foraging (Brown, 1999; Camp et al., 2012; Lima & Dill, 1990). Behaviors measured during the in-hand tests also covaried among individuals in both Hinton's (2022) analysis and in ours. Collectively, behaviors measured during the in-hand tests have been interpreted to represent post-capture predator defense strategies (Hinton, 2022), where struggling and tonic immobility (also known as feigning death) are two steps in the post-capture predator escape sequence (Golubović et al., 2021; Humphreys & Ruxton, 2018; Sargeant & Eberhardt, 1975). Hinton (2022) provides a more extensive discussion of the ecological relevance of the open field and in-hand tests.

Both morphology and behavior often are important influences of the general success (i.e., survival) and long-term fitness of many species of wildlife (Monaghan, 2008; Montiglio et al., 2018; Réale et al., 2010; Ricklefs & Wikelski, 2002). Previous studies both in wood ducks and other waterfowl found positive relationships between size and measures of fitness such as survival, reproductive success, and lifetime fecundity (Anderson & Alisauskas, 2001; Cooch, 2002; Mangel & Stamps, 2001; B. S. Sedinger et al., 2018; J. S. Sedinger et al., 1995; J. S. Sedinger & Chelgren, 2007). Interestingly, we were unable to identify any single morphological variable that significantly influenced birds' survival to adulthood. Behavior, specifically *tonic alertness*, appeared to have some influence on survival, however, the effect was subtle. When morphology and behavior were combined collectively in multi-variable models, both affected

survival. Although no single variable in our models had a sole influence, cumulatively, we found that behavior was more influential than morphology for most measures of fitness that we examined. This trend surprised us initially, given the evidence suggesting an influence of size on survival and reproductive success in waterfowl (Anderson & Alisauskas, 2001; Dawson & Clark, 1996, 2000; Rotella et al., 2003; B. S. Sedinger et al., 2018; J. S. Sedinger et al., 1995; J. S. Sedinger & Chelgren, 2007). That said, we attribute the captive environment to reducing or removing selective pressures that free-living birds would otherwise encounter making size less relevant. Indeed, it might be reasonable to expect that captive-rearing in a benign common garden environment might minimize or eliminate some longer-term effects of early life growth or size. The fact that we found long-term influence of morphological and especially behavioral variation, is perhaps the more surprising outcome, suggesting that the consequences of individual differences in these early life patterns cannot be fully eliminated in a captive setting. This has implications both for better understanding the influence of inter-individual variation and also for captive-rearing conservation programs (see more below).

We also found some evidence that both morphology and behavior influenced the *number of years that individuals were detected* in our study populations after release. Interestingly, post-release longevity seemed to be the only instance where early life morphology strongly influenced long-term individual fitness. Here, there was indication that *initial size* (e.g., larger duckling size) was negatively related to number of years detected post release (Figure 8; Table 5). Based on previous research of free-living waterfowl, larger offspring tend to experience increased rates of survival (Anderson & Alisauskas, 2001; Dawson & Clark, 1996, 2000; B. S. Sedinger et al., 2018; J. S. Sedinger et al., 1995; J. S. Sedinger & Chelgren, 2007). However, Rotella et al. (2003), found that heavier ducklings had lower survival than lighter individuals in one

population of Lesser Scaup. Regarding our study, one plausible explanation is a size versus longevity tradeoff, whereby individuals invest early in size at the expense of lifespan, akin to the pace-of-life syndrome hypothesis (Monaghan, 2008; Montiglio et al., 2018; Réale et al., 2010; Ricklefs & Wikelski, 2002). Accordingly, fast growth leading to larger size may improve chances of survival early in life, but at the cost of reduced lifespan. In contrast, slower growth and smaller size may reduce early chances of survival, but individuals may benefit from a longer life should they survive to adulthood.

We realize that the relationships among size, growth, and longevity may have been influenced by the captive environment. A greater number of slow growing individuals may have survived the first few weeks of life such that, when released, we were better able to detect their enhanced longevity. In wild, free-living birds, many of these slow-growing individuals may not have survived the first few weeks of life, rendering it statistically challenging to detect effects on longevity. Söderquist et al. (2013) found that in mallards, wild individuals lived longer than those that were reared in captivity and then released. Thus, it is plausible that captive-rearing influences longevity quite differently than uncontrolled, natural conditions. Further investigation is needed to fully understand this dynamic in wood ducks.

In terms of reproductive strategy, we found evidence that both morphology and behavior influenced reproductive performance. *Tonic alertness*, *response intensity*, and *space use* were all predictive of *number of years incubating*. We could not develop a plausible explanation for any direct ecological or behavioral connection between tonic immobility and the decision of whether to establish and incubate a nest. We explored the possibility that this relationship was indirectly influenced by individual longevity, but there was no relationship between longevity (*number of years detected*) and *tonic alertness*. The negative relationship of *number of years incubating* with

response intensity and the positive relationship with *space use* are more easily understood. Hinton's (2022) interpretations of *response intensity* and *space use* was that they measured different aspects of behavior related to risk management. Here, we found that individuals that exhibited a lower intensity response to threatening stimuli and that were more willing to risk danger to explore their environment were also more likely to incubate nests. Therefore, it is plausible that individuals' risk tolerance would influence their decision to initiate and incubate a nest. For most bird species, nesting and incubating eggs can be inherently risky (Martin, 1995; Ricklefs, 1969). In a system that includes an alternative reproductive strategy to nesting and incubating one's own eggs (conspecific brood parasitism), underlying behavioral characteristics – such as willingness to accept risk – may well influence which strategy an individual employs. The decision to engage in parasitic egg laying and skip incubation, or to forego reproduction altogether in a given year, may be a simple extension of risk averse behavior. Furthermore, these relationships may also explain the correlation between *tonic alertness* and *number of years incubating*. Covariation of behavioral traits is common in many species (Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, et al., 2004). These behavioral syndromes often result in correlated but otherwise unrelated behaviors. Accordingly, *tonic alertness* may simply be a trait that covaried with *response intensity* or *space use* but otherwise has no direct relationship with reproductive decision making.

We did not detect any influence of morphology or behavior on birds' nest box visitation rates. This result was somewhat surprising. Nest box location and quality can have important implications for safety and nest success (Martin, 1993). Furthermore, we know that female wood ducks show considerable individual variation in the number of nest boxes that they visit during the breeding season (Eadie et al., unpublished data). Thus, we anticipated a potential relationship

with either behavior or morphology, but perhaps the patterns we observed were more likely influenced by environmental conditions rather than individual characteristics.

Our investigation of reproductive investment and success considered the variables *average clutch size*, *number of successful nesting years*, and *number of ducklings produced*. For both *average clutch size* and *number of ducklings produced*, behavior appeared to be most influential, however, supporting evidence was limited. The exception was our finding indicating that both behavior and morphology had some influence on how many eggs an individual produces and lays. Although *response intensity* was the most strongly weighted variable, the ecological connection between behavioral *response intensity* and clutch size was not so clear. In contrast, however, was the fact that both morphology and behavior affected the number of successful nesting years by an individual. Here, *response intensity* predicted the number of successful nesting years, where individuals that displayed lower *response intensity* had more successful nesting years. This outcome seems to align with a risk sensitivity perspective. In other words, individuals that respond more intensely to threatening stimuli may be less likely to behave optimally while nesting. For instance, these individuals may be more prone to flush from nests compared to individuals that respond with lower intensity, or delay returning to a nest after being alarmed, which could lead to frequent temperature fluctuations during incubation. Consistency in incubation temperature is correlated with both hatch and post-hatch success in many bird species (Durant et al., 2010; DuRant et al., 2011, 2012; Durant et al., 2013; Hopkins et al., 2011; Manlove & Hepp, 2000; Webb, 1987).

Generally, our study provides evidence that individual variation in morphology and behavior can influence several aspects of individual fitness for captive-reared wood ducks. Overall, behavioral traits seemed to be most influential in predicting longer-term measures of

success. Morphological traits, mostly, were not predictive of long-term fitness, with the one exception that initial duckling size was negatively related to longevity. The strongest patterns detected were positive relationships between early life size and growth rates and individual covariation in behaviors. Both morphological and behavioral traits often appeared to influence longer-term measures of fitness, although we could not separately parse influences of specific traits in many cases. This is not entirely unexpected perhaps, given that we anticipated that captive-rearing may have moderated or overridden the influence of individual differences in morphology and behavior. As noted above, perhaps it is more revealing that several early life morphological and behavioral traits maintained an influence on birds' fledging size and reproductive success later in life. These influences, for the most part, appeared small and often detectable only in multi-variable models. However, because these effects were detected at all, and the consistency with which behavior-only models were among the top models in almost all analyses, suggests that individual differences in behavioral phenotype may be important to future reproductive success and survival of wood ducks, and perhaps other precocial birds. Further investigation is needed to differentiate the relative effect of each individual trait. Perhaps the strongest tests would comprise studies that monitor size, growth, and behavior through ontogeny among individuals in the wild, where the effects of predation and food limitation are operational. This approach, however, would be logistically challenging without new advances in technology that allow remote monitoring and non-invasive repeated sampling. An alternative study would be to create more natural conditions in captivity where greater levels of predation risk or food limitation are simulated (see Hinton, 2022).

Conservation Applications

We believe our study forwards important implications for conservation and captive avian breeding programs. We observed considerable variation among individual wood ducks in hatch size, growth rate, and fledging size, despite common garden rearing conditions that were predator free and contained unlimited food. Given this variation, we anticipated that we would detect some influence on survival to adulthood. However, we found no relationship between any measure of growth or morphology and survival to adulthood in our captive-reared individuals after they were released into the wild. These results seem inconsistent with previous waterfowl literature where larger, faster growing individuals tend to experience greater survival to adulthood in most cases. There is at least one notable exception to these trends, were Rotella et al. (2003) found that Lesser Scaup of lighter mass survived better than heavier ducklings. Our findings indicate that any size advantages experienced by ducklings may be most consequential for survival only in the first several weeks of life. Our results suggest that it is possible to ameliorate early life mortality, resulting from initial disadvantages in size, by raising ducks to at least fledging age (5 weeks) in captivity. Eliminating predation and starvation pressures under captive conditions removes or at least reduces a major survival bottleneck. Our novel use of RFID technology allowed us to detect all released females in our study including non-breeding individuals that would otherwise not be counted, which subsequently enhanced our estimates of survival of the captive-reared individuals. RFID detection is a huge improvement in accuracy over other detection methods giving us far better insight into the effectiveness of captive-rearing. The findings from this study provide new empirical information that can help guide and inform future captive-breeding and conservation programs for ducks and other waterfowl.

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Figure 1. Image of the behavioral arena used for the open field tests.

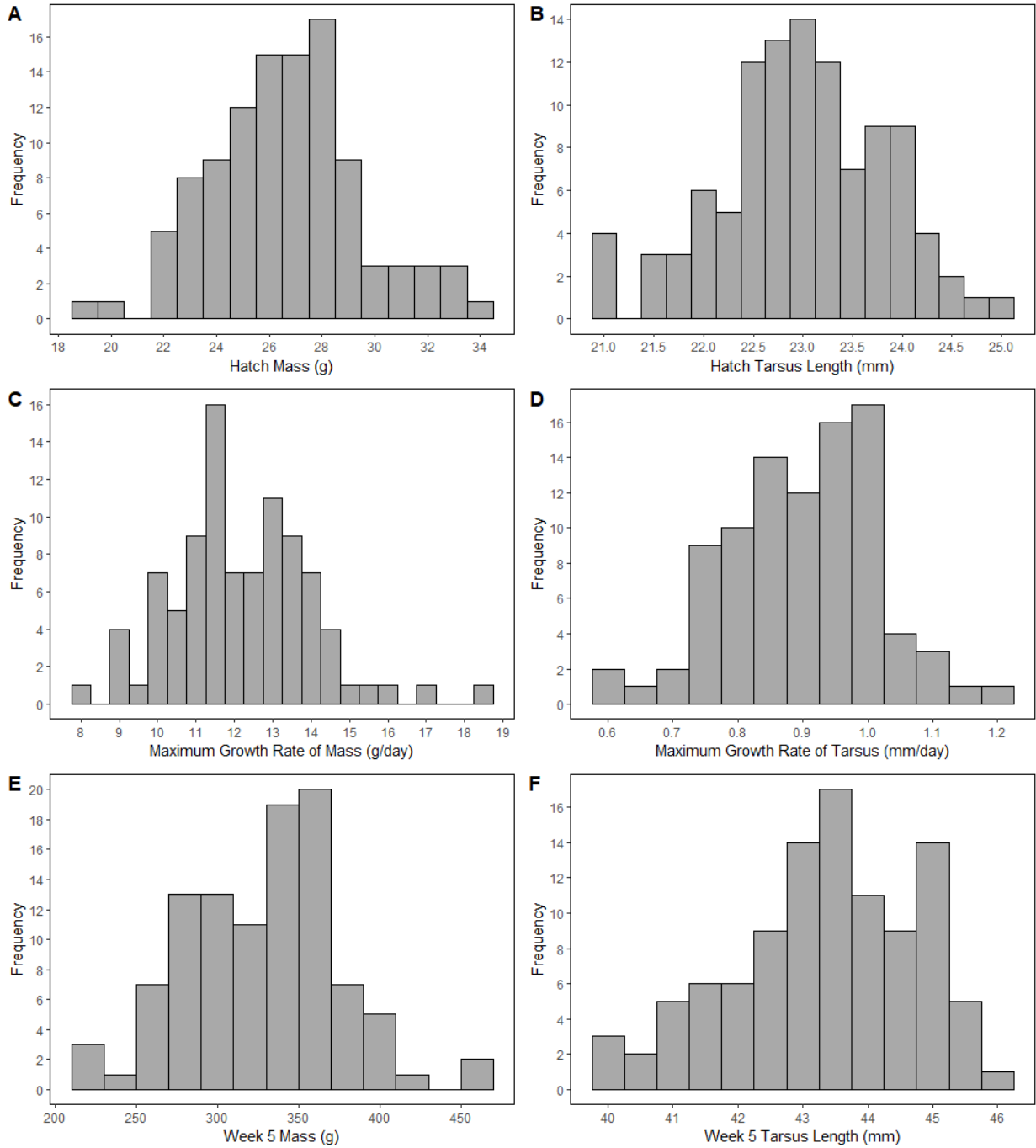


Figure 2. Individual variation in morphological measures of female wood ducks that were reared in a common garden environment.

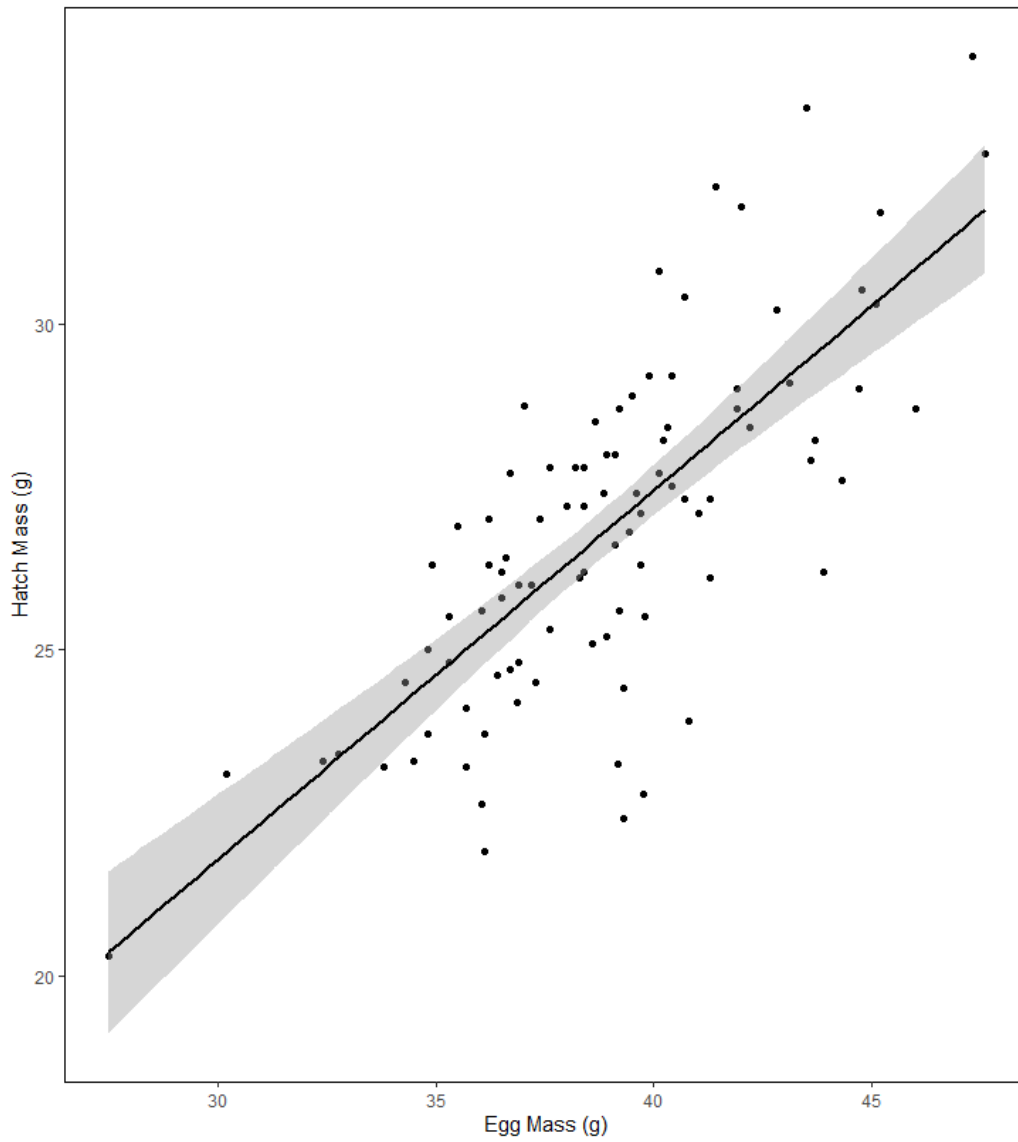


Figure 3. Positive relationship between egg mass and hatch mass for captive-reared female wood ducks ($R^2 = 0.55$, $P < 2e-16$). The shaded area indicates confidence around the trendline.

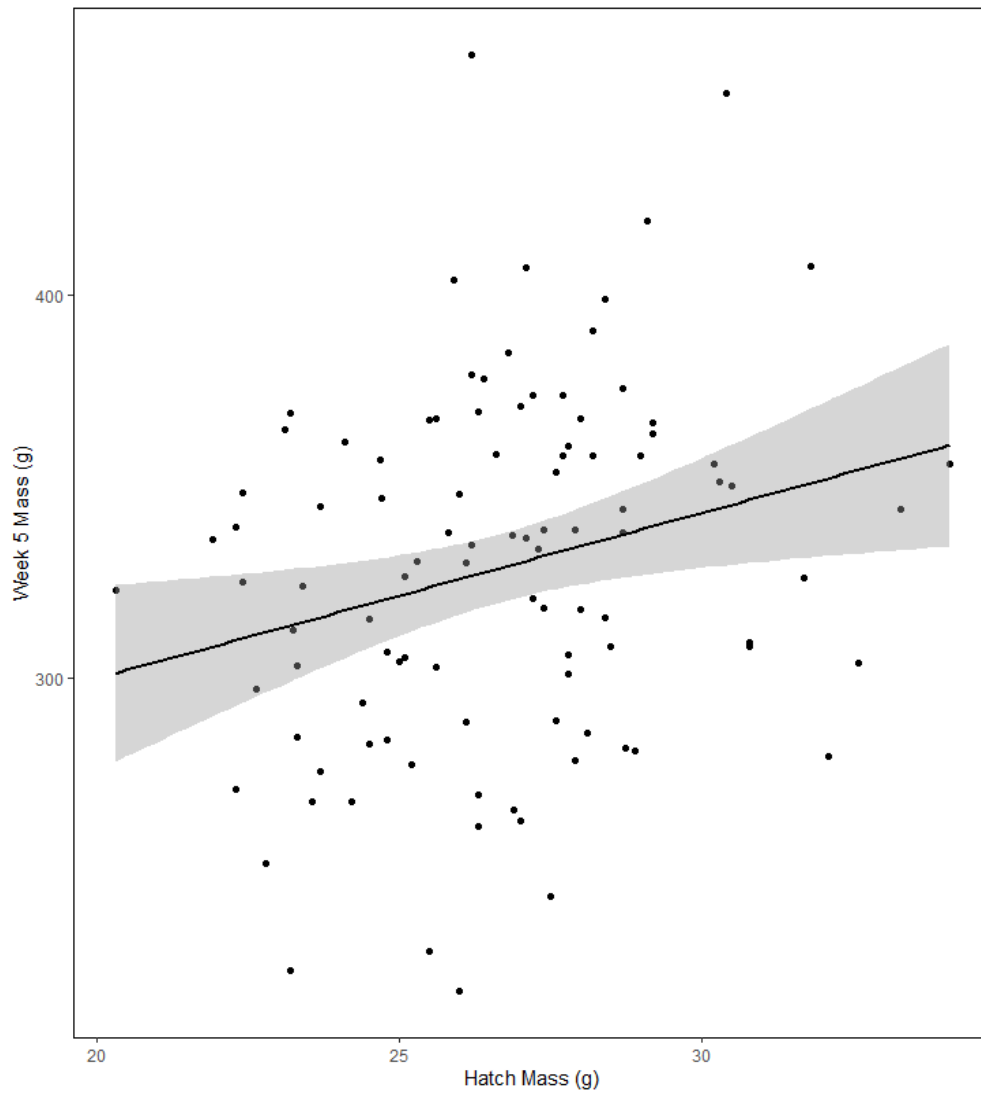


Figure 4. Positive relationship between hatch mass and week 5 mass for captive-reared female wood ducks ($R^2 = 0.05$, $P = 0.01$). The shaded area indicates confidence around the trendline.

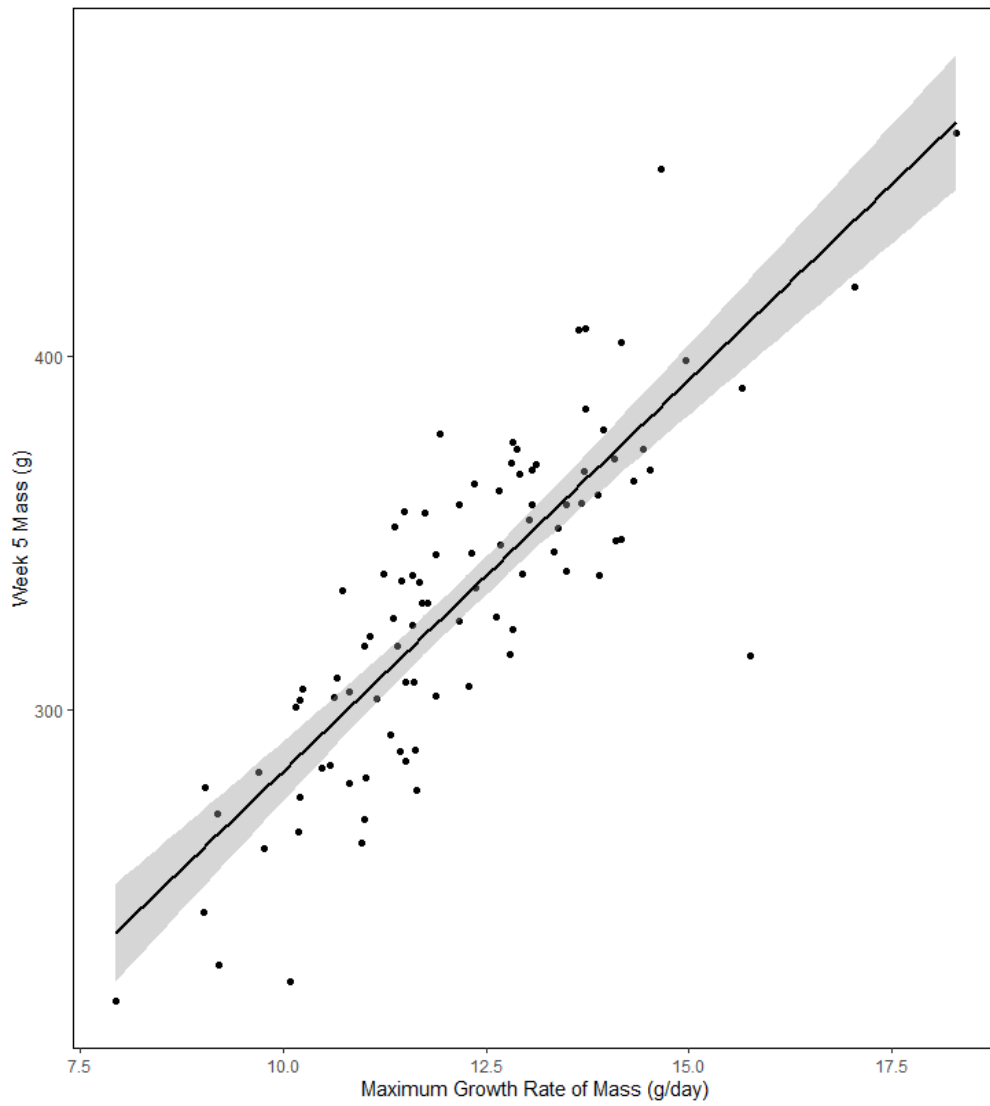


Figure 5. Positive relationship between maximum growth rate of mass and week 5 mass for captive-reared female wood ducks ($R^2 = 0.70$, $P < 2e-16$). The shaded area indicates confidence around the trendline.

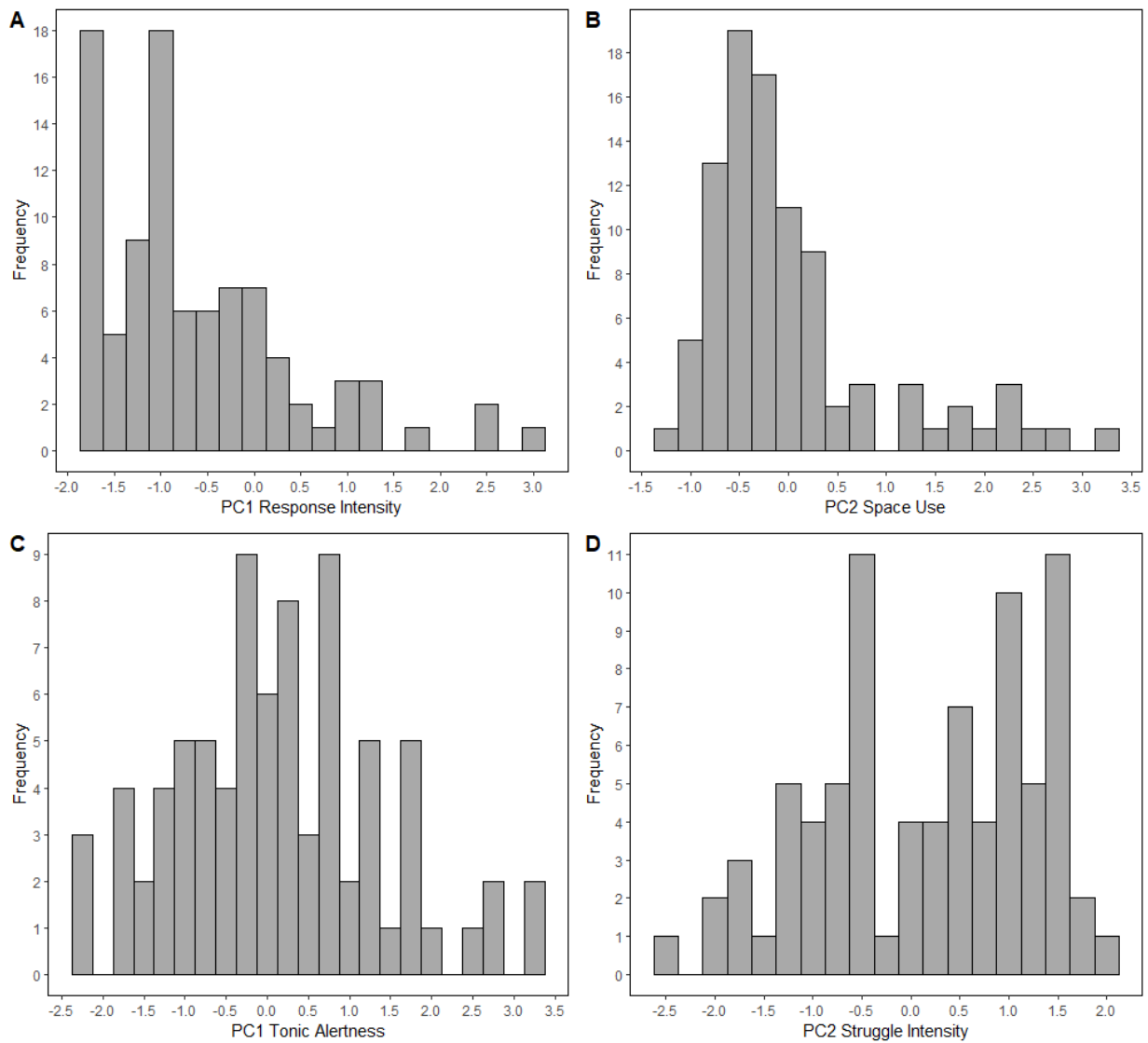


Figure 6. Individual variation in behavioral measures of female wood ducks that were reared in a common garden environment. PC1 Response Intensity (panel A) and PC2 Space Use (B) were measured in open-field tests. PC1 Tonic Alertness (panel C) and PC2 Struggle Intensity (D) were measured using in-hand tests.

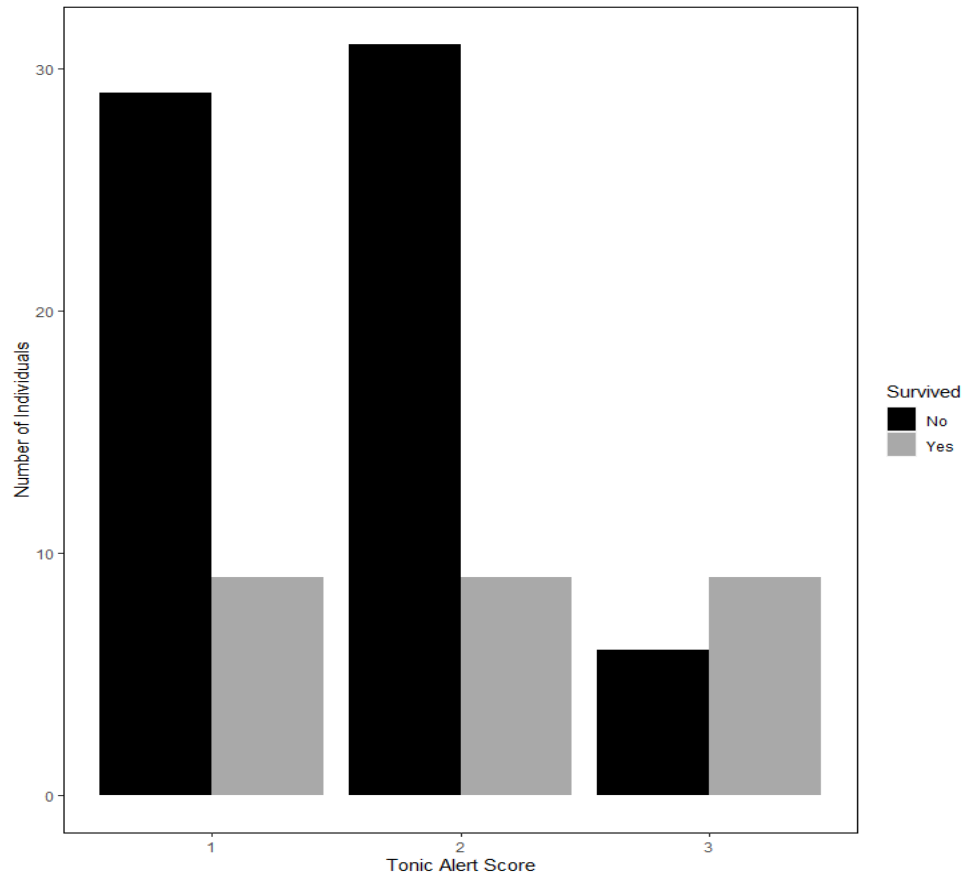


Figure 7. Relationship between tonic alert score and survival. As tonic alert score increased survival also increased (slope estimate 0.686, $P = 0.04$).

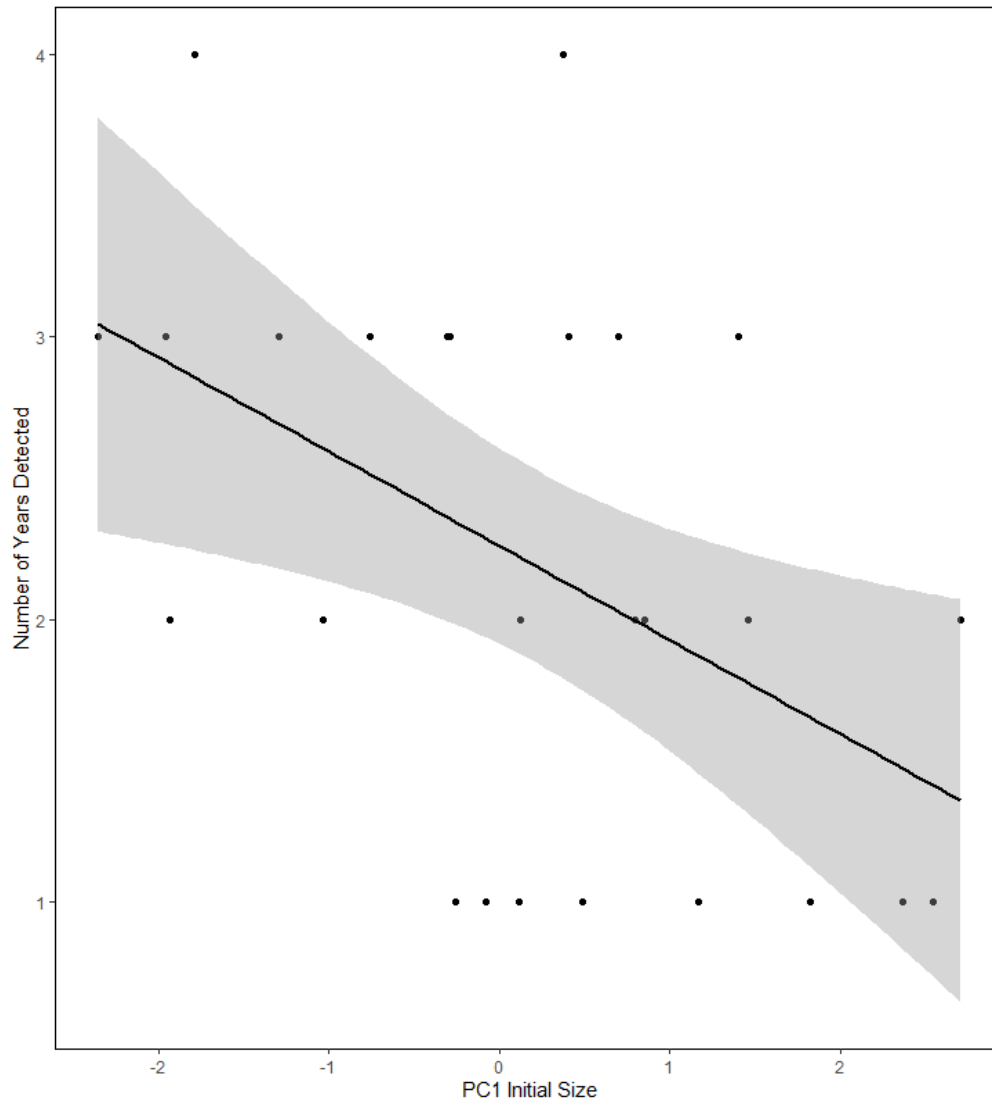


Figure 8. Negative relationship between PC1 Initial Size and number of years detected post release for captive-reared female wood ducks (slope estimate = -0.31, 95% CI [-0.62, -0.01]). The shaded area indicates confidence around the trendline.

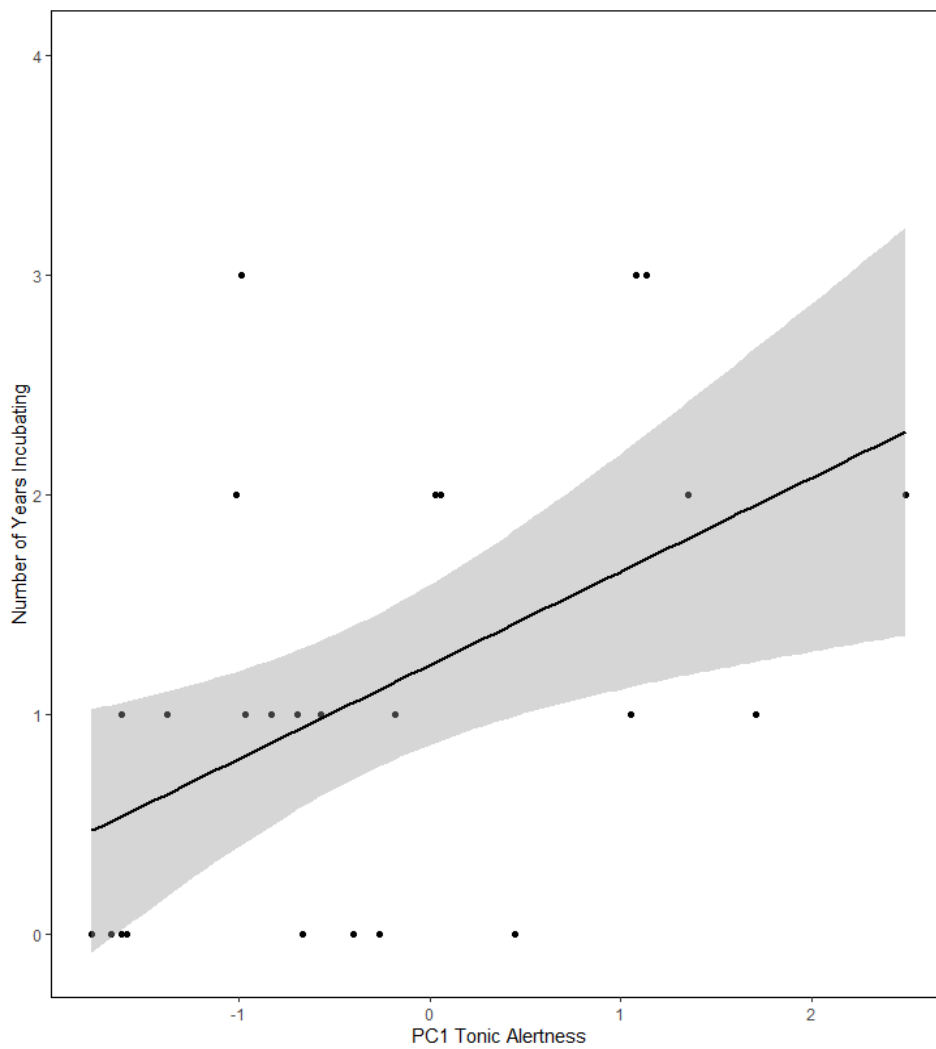


Figure 9. Positive relationship between PC1 Tonic Alertness and number of years incubating for captive-reared female wood ducks (slope estimate = 0.54, 95% CI [0.20, 0.87]). The shaded area indicates confidence around the trendline.

Table 1. Principal Component Analysis loading scores for morphological measurements. Measurements of egg and hatch size loaded positively on PC1 such that an increase in PC1 corresponds with an increase in egg mass, hatch mass, and hatch tarsus length. Maximum growth rates loaded positively on PC2, such that an increase in PC2 corresponds with an increase in maximum growth rate of both mass and tarsus length.

Morphological Size and Growth		
	PC1: Initial Size	PC2: Growth Rate
Egg Mass	0.875	-0.143
Hatch Mass	0.830	-0.209
Hatch Tarsus	0.802	-0.119
Maximum Growth Rate Mass	0.285	0.835
Maximum Growth Rate Tarsus	0.180	0.864

Table 2. Eigen decomposition loading scores for open field and in hand test behavioral measurements. For open field test behaviors, activity, startle response, and response to the observer all loaded positively on PC1 such that an increase in PC1 corresponds with an increase in activity and intensity of response to both stimuli. Revisitation of the initial startle stimulus (removal of the acclimation chamber) and anti-thigmotaxis loaded positively on PC2 such that an increase in PC2 corresponds with an increase in the overall amount of space that individuals are willing to explore. For in hand behaviors, all three measurements related to tonic immobility loaded on PC1 such that an increase in PC1 corresponds with increases in both alertness while in a tonic state and number of attempts required to induce tonic immobility and a decrease in the duration of tonic immobility. Number of struggling bouts initiated during the struggle test loaded positively on PC2 such that an increase in PC2 corresponds with an increase in number of struggling bouts or struggle intensity.

Open Field Test Behavioral Measures		
	PC1: Response Intensity	PC2: Space Use
Startle Stimulus Revisitation	-0.118	0.702
Anti-Thigmotaxis	0.336	0.599
Activity	0.547	0.221
Startle Response	0.562	-0.243
Response to Observer	0.508	-0.202
In Hand Behavioral Measures		
	PC1: Tonic Alertness	PC2: Struggle Intensity
Tonic Alertness	0.574	-0.111
Tonic Attempts	0.528	-0.083
Tonic Duration	-0.608	0.065
Struggle Test	0.149	0.988

Table 3. Results of binomial generalized linear models investigating the relationship between survival and individual morphological traits. Bolded items indicate a significant relationship with survival, where applicable.

Influence of Morphological Traits on Survival				
Predictor Variable	Estimate	Std. Error	Z-value	P-value
Egg Mass	0.034	0.063	0.54	0.59
Hatch Mass	0.012	0.075	0.17	0.87
Hatch Tarsus	0.201	0.257	0.78	0.44
Week 5 Mass	0.001	0.005	0.22	0.83
Week 5 Tarsus	0.039	0.155	0.25	0.80
Max Growth Rate Mass	0.029	0.129	0.22	0.83
Max Growth Rate Tarsus	-0.075	2.016	-0.04	0.97

Table 4. Results of binomial generalized linear models investigating the relationship between survival and individual behavioral traits. Bolded items indicate a significant relationship with survival, where applicable.

Influence of Behavioral Traits on Survival				
Predictor Variable	Estimate	Std. Error	Z-value	P-value
Tonic Attempts	0.157	0.212	0.74	0.46
Tonic Alert	0.686	0.327	2.09	0.04
Tonic Immobility Duration	-0.010	0.011	-0.89	0.38
Struggle Test	-0.009	0.046	-0.19	0.85
Startle Response	0.014	0.248	0.06	0.96
Response to Observer	0.535	0.309	1.73	0.08
Anti-Thigmotaxis	0.805	1.595	0.51	0.61
Startle Stimulus Revisitation	-1.385	1.046	-1.32	0.19
Activity	-0.002	0.003	-0.85	0.39

Table 5. Model results from multi-variable analyses of the influence of morphology and behavior on survival and longevity. Top ranked models determined by Akaike Information Criterion (AIC) values. Weights for each predictor variable summed across all models shown in “Variable Weight” Column.

Survival to Adulthood (Binomial GLM)							
Model	AIC	ΔAIC	Variable Weight	Variable	Estimate	95% CI	
Full	97.93	0	0.440	PC1 Initial Size	0.04	-0.32, 0.41	
			0.440	PC2 Growth Rate	0.18	-0.26, 0.64	
			0.652	PC1 Tonic Alertness	0.42	-0.06, 0.92	
			0.652	PC2 Struggle Intensity	-0.46	-1.35, 0.27	
			0.778	PC1 Response Intensity	-0.21	-0.70, 0.23	
Behavioral Variables	99.35	1.42		PC1 Tonic Alertness	0.38	-0.07, 0.86	
				PC2 Struggle Intensity	-0.48	-1.28, 0.17	
				PC1 Response Intensity	-0.22	-0.69, 0.21	
				PC2 Space Use	0.33	-0.15, 0.84	
Morphological Variables	110.53	12.60		PC1 Initial Size	0.06	-0.26, 0.39	
				PC2 Growth Rate	0.04	-0.35, 0.43	
Intercept Only	133.47	35.54		Intercept	-0.79	-1.22, -0.39	
Number of Years Detected							
Model	AIC	ΔAIC	Variable Weight	Variable	Estimate	95% CI	R-squared
Full	71.75	0	0.212	PC1 Initial Size	-0.31	-0.62, -0.01	0.29
			0.140	PC2 Growth Rate	0.02	-0.31, 0.35	
			0.173	PC1 Tonic Alertness	0.23	-0.17, 0.62	
			0.170	PC2 Struggle Intensity	0.03	-0.91, 0.97	
			0.515	PC1 Response Intensity	-0.17	-0.62, 0.29	
Behavioral Variables	72.99	1.24		PC1 Tonic Alertness	0.21	-0.20, 0.63	0.10
				PC2 Struggle Intensity	-0.24	-1.08, 0.61	
				PC1 Response Intensity	-0.10	-0.57, 0.37	
				PC2 Space Use	0.10	-0.39, 0.60	
Morphological Variables	74.45	2.70		PC1 Initial Size	-0.33	-0.58, -0.08	0.23
				PC2 Growth Rate	-0.02	-0.27, 0.22	
Intercept Only	98.69	26.94		Intercept	2.24	1.89, 2.59	

Table 6. Model results from multi-variable analyses of the influence of morphology and behavior on reproductive strategy. Top ranked models determined by Akaike Information Criterion (AIC) values. Weights for each predictor variable summed across all models shown in “Variable Weight” Column.

Number of Years Incubating							
Model	AIC	ΔAIC	Variable Weight	Variable	Estimate	95% CI	R-squared
Full	64.37	0	0.592	PC1 Initial Size	-0.26	-0.52, -0.0009	0.54
			0.591	PC2 Growth Rate	0.06	-0.22, 0.34	
			0.944	PC1 Tonic Alertness	0.54	0.20, 0.87	
			0.939	PC2 Struggle Intensity	0.18	-0.63, 0.98	
			0.952	PC1 Response Intensity	-0.43	-0.82, -0.04	
Behavioral Variables	65.43	1.06		PC1 Tonic Alertness	0.53	0.18, 0.88	0.42
				PC2 Struggle Intensity	0.003	-0.71, 0.72	
				PC1 Response Intensity	-0.37	-0.77, 0.03	
				PC2 Space Use	0.49	0.07, 0.91	
Morphological Variables	79.50	15.14		PC1 Initial Size	-0.27	-0.54, 0.004	0.14
				PC2 Growth Rate	0.07	-0.20 0.34	
Intercept Only	108.26	43.89		Intercept	1.21	0.81, 1.62	
Proportion of Total Nest Boxes Visited							
Model	AIC	ΔAIC	Variable Weight	Variable	Estimate	95% CI	R-squared
Intercept Only	-61.24	0		Intercept	0.16	0.13, 0.19	
Morphological Variables	-42.48	18.76		PC1 Initial Size	0.004	-0.02, 0.03	0.05
				PC2 Growth Rate	-0.01	-0.04, 0.01	
Behavioral Variables	-36.99	24.25		PC1 Tonic Alertness	-0.03	-0.06, 0.01	0.19
				PC2 Struggle Intensity	-0.06	-0.13, 0.01	
				PC1 Response Intensity	0.01	-0.03, 0.06	
				PC2 Space Use	-0.03	-0.07, 0.02	
Full	-33.00	28.24	0	PC1 Initial Size	-0.0002	-0.03, 0.03	0.19
			0	PC2 Growth Rate	0.001	-0.03, 0.03	
			0	PC1 Tonic Alertness	-0.03	-0.07, 0.01	
			0	PC2 Struggle Intensity	-0.06	-0.15, 0.03	
			0	PC1 Response Intensity	0.01	-0.03, 0.06	
			0	PC2 Space Use	-0.03	-0.08, 0.02	

Table 7. Model results from multi-variable analyses of the influence of morphology and behavior on reproductive investment and success. Top ranked models determined by Akaike Information Criterion (AIC) values. Weights for each predictor variable summed across all models shown in “Variable Weight” Column.

Average Clutch Size							
Model	AIC	ΔAIC	Variable Weight	Variable	Estimate	95% CI	R-squared
Behavioral Variables	18.54	0		PC1 Tonic Alertness	1.06	0.82, 1.37	0.21
				PC2 Struggle Intensity	0.89	0.49, 1.61	
				PC1 Response Intensity	1.05	0.80, 1.39	
				PC2 Space Use	1.05	0.79, 1.39	
Full	19.02	0.48	0.054	PC1 Initial Size	1.07	0.95, 1.21	0.37
			0.056	PC2 Growth Rate	0.93	0.79, 1.09	
			0.099	PC1 Tonic Alertness	1.05	0.81, 1.35	
			0.103	PC2 Struggle Intensity	0.91	0.50, 1.64	
			0.707	PC1 Response Intensity	1.08	0.82, 1.42	
			0.366	PC2 Space Use	1.04	0.78, 1.39	
Morphological Variables	22.54	4.00		PC1 Initial Size	1.09	0.97, 1.24	0.26
				PC2 Growth Rate	0.87	0.75, 1.01	
Intercept Only	31.17	12.63		Intercept	14.23	11.75, 17.24	
Number of Successful Nesting Years							
Model	AIC	ΔAIC	Variable Weight	Variable	Estimate	95% CI	R-squared
Full	32.60	0	0.456	PC1 Initial Size	-0.16	-0.39, 0.08	0.58
			0.442	PC2 Growth Rate	0.20	-0.13, 0.53	
			0.532	PC1 Tonic Alertness	0.50	-0.02, 1.02	
			0.532	PC2 Struggle Intensity	0.53	-0.64, 1.69	
			0.802	PC1 Response Intensity	-0.56	-1.02, -0.09	
			0.684	PC2 Space Use	0.40	-0.13, 0.93	
Behavioral Variables	35.56	2.95		PC1 Tonic Alertness	0.45	-0.08, 0.99	0.31
				PC2 Struggle Intensity	0.52	-0.75, 1.79	
				PC1 Response Intensity	-0.50	-1.02, 0.03	
				PC2 Space Use	0.37	-0.22, 0.96	
Morphological Variables	40.52	7.91		PC1 Initial Size	-0.20	-0.43, 0.03	0.20
				PC2 Growth Rate	0.09	-0.21, 0.39	
Intercept Only	56.46	23.86		Intercept	1.38	1.01, 1.75	
Number of Ducklings Produced							
Model	AIC	ΔAIC	Variable Weight	Variable	Estimate	95% CI	R-squared
Behavioral Variables	67.44	0		PC1 Tonic Alertness	8.63E-06	-0.04, 0.06	0.12
				PC2 Struggle Intensity	-0.004	-0.75, 0.20	
				PC1 Response Intensity	-0.03	-0.37, 0.002	
				PC2 Space Use	0.001	-0.04, 0.15	
Full	68.97	1.53	0.023	PC1 Initial Size	0.00003	-0.02, 0.03	0.21
			0.023	PC2 Growth Rate	0.009	-0.001, 0.14	
			0.071	PC1 Tonic Alertness	-1.61E-09	-0.05, 0.05	
			0.071	PC2 Struggle Intensity	-0.09	-2.41, 0.08	
			0.770	PC1 Response Intensity	-0.04	-0.44, 0.001	
			0.298	PC2 Space Use	1.56E-06	-0.09, 0.10	
Morphological Variables	78.92	11.48		PC1 Initial Size	0.001	-0.006, 0.05	0.02
				PC2 Growth Rate	-3.37E-07	-0.02, 0.02	
Intercept Only	93.96	26.52		Intercept	1.26	0.43, 2.79	