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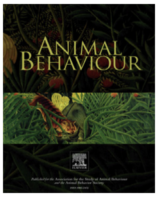

The older the bolder: common goldeneye antipredator behaviour based on long-term individual data

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Long-term individual-based studies of parental investment are pivotal to understanding the costs and benefits associated with defensive strategies under stressful conditions. In the context of avian research, limited literature exists on longitudinal changes in antipredator behaviour during incubation and potential selection pressures on a specific trait. We studied the response of common goldeneye, *Bucephala clangula*, to disturbance, mimicking a predation threat in a nestbox population from 1984 to 2021. From a total of 652 captured females, 516 were recaptured as breeders 2–15 times over the study period. During the nest-monitoring visits, female behaviour was classified as ‘shy’ (flushing before the human observer reached the nestbox, or they flew into the net placed over the nest hole), ‘average’ (leaving the nest when the observer scratched the nestbox wall, or they showed inconsistent flush patterns such as once behaving shy and once bold in the same year), or ‘bold’ (leaving the nest once physically touched or they did not leave at all). Our results provide evidence of plasticity of antipredator behaviour, since the probability of exhibiting a bold reaction to a perceived predation danger increased with age, whereas shy individuals became less common. On the other hand, we found a high level of repeatability of behavioural response across individuals. The findings reveal the coexistence of plastic and personality traits among common goldeneye females. Moreover, there was a positive linear interaction between age and clutch size on boldness, but only for clutches below the parasitism threshold (fewer than 13 eggs). Interestingly, hatching success was not related to behaviour, suggesting no direct selection pressure on antipredator behaviour and that depending on age/residual reproductive value, either shy or bold types are favoured to benefit the lifetime reproductive success of individuals.

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The dynamic of animals’ responses to environmental risks has long fascinated researchers (Kohl et al., 2018; Lima & Bednekoff, 1999). Dangers associated with the microhabitat of organisms affect internal (physiology, immune system) and external (morphology and behaviour) traits, in turn playing a role in fitness and survival (Ibanez-Alamo et al., 2015). Predation serves as a significant threat, not only imposing selective pressure on the animal’s behaviour on an evolutionary scale but also shaping its lifetime decision making (Lima & Dill, 1990). In birds, incubation is a vulnerable period, exposing them to increased predation risk (Fontaine & Martin, 2006). While nest defence against predation has historically received much attention, little is known about how it interacts with other aspects of parental decision making, such as the escape strategy against predators (Lima, 2009). The drivers of the decision to escape are strongly influenced by the animal’s ability to perceive and modify its response on a state and context basis. This indicates that individuals under risk of predation face a trade-off between reproductive investment and survival (Moller et al., 2013). The causal framework behind the trade-off between maximizing self-survival and reproductive output during incubation needs to be further understood, particularly in the context of long-term studies. Reproductive investment trade-offs, particularly in long-lived species, are influenced by numerous variables. These

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include, for example, individual quality (higher survival rate of successful breeders compared to unsuccessful ones; Lescroël et al., 2009), yearly fluctuations in the habitat condition (variation in clutch size between years; Griesser et al., 2017), and variation in predation risk (effects on the frequency of nest visits by parents; Eggers et al., 2005). In this study, we explored the long-term trajectory of antipredator behaviour, measured by escape decisions under a perceived predation danger.

Understanding the plasticity of an individual's behaviour under stressful conditions is also important for conservation purposes by giving predictions on how perceived risk from predators and humans may have important population demographic consequences (Gaynor et al., 2021). We studied the between-years trend in antipredator behaviour of common goldeneye, *Bucephala clangula,* a species of sea duck whose breeding population is declining in Finland (Piha & Lindén, 2023). The nest defence strategy of incubating parents involves complex choices influenced by factors such as previous experience, endocrine-based stress response and individual-specific behavioural traits (e.g. shyness and boldness levels; Moller et al., 2013; Seltmann, 2014; Mohring et al., 2021). However, predation risk is not the only ecological context in which the defensive response of egg-laying or incubating females to intruders may have fitness consequences. Our study also took into account the effect of brood parasitism as a type of parental-care parasitism in which females lay eggs in the nests of other females of the same or different species (Medina & Langmore, 2016; Petrie & Møller, 1991). As brood parasites impose fitness costs on host females, hosts have evolved numerous ways of defence, including direct nest defence against parasites (e.g. Roldán & Soler, 2011; Soler, 2017). Hence, in species with frequent conspecific brood parasitism (CBP), nest defence against parasites might be behaviourally evolved, similar to antipredator behaviour.

Age is a fundamental factor influencing behavioural responsiveness in many species. As individuals mature, they learn from previous experience and gain more knowledge about their environment leading to modification of responses to a predation threat (Gosling, 2001; Urszán et al., 2018). These responses could vary from a behavioural response to danger to dispersal to a new breeding location (Lima, 2009; Stamps et al., 2010). Previous research shows that within a single breeding season, female common goldeneye exhibit a stronger nest defence response as the hatch date approaches when faced with human intruders (Mallory et al., 1998). However, the influence of previous years' exposure on future nest defence remains unclear. It is crucial to investigate the longitudinal change in antipredator behaviour with age to uncover the developmental trajectory of individuals and the role of experience in shaping adaptive responses.

According to parental investment theory, nest care effort is linked to the reproductive value of the current brood (e.g. relative parental investment based on the severity of egg loss rather than the stage of incubation; Ackerman & Eadie, 2003), likelihood of survival (lower abandonment rate in species with higher mortality rate and higher breeding output; Forbes et al., 1994), previous exposure to predation (change in brood-rearing effort in relation to previously experienced brood mortality, Pöysä et al., 1997; change in nest location, Fontaine & Martin, 2006), as well as future reproductive opportunities (skipping a breeding season after prolonged nest attendance in the previous season; Osorno & Osorno, 1999). Age-dependent increase in parental investment has been proposed based on the hypothesis that older individuals of low future reproductive value invest more in the current breeding attempt (Duffield et al., 2017). Self-survival is expected to be prioritized in long-lived species in favour of future reproduction (Ghalambor & Martin, 2000), as reflected in bolder responses of older individuals to an observer, for example in female barnacle geese, *Branta leucopsis* (de Jong et al., 2021). The current study on a long-lived sea duck species explores the extent to which ageing and variation in clutch size shape the antipredator behaviour throughout the breeding life span.

Another facet of antipredator behaviour is nest parasitism. Åhlund (2005) revealed variations in how host females respond to intruding brood parasites in common goldeneye. While most hosts defended their nest against parasites, the possible low cost of being parasitized for some females might dampen the defence. However, the possible connection between host female antipredator behaviour and CBP has not been studied before, using data from individually known females, specifically, whether the rate of parasitic laying is associated with host female defence behaviour (see also Mallory et al., 1998). In other words, research is needed to explore whether female behaviour/personality type affects the probability of getting parasitized. Our study followed this question while simultaneously considering female traits of age or breeding experience. Exploring the effect of age-dependent variation in clutch size on nest defence provides insight into the trade-offs that individuals face when allocating resources to reproduction and self-survival. Moreover, understanding the interaction between clutch size and age in shaping antipredator responses helps with comprehending the complexities of reproductive decision making.

Long-term tracking of individual responses in challenging environments provides comprehensive insights into behavioural changes over time and potential selection pressures on phenotypic traits (Clutton-Brock & Sheldon, 2010; Husby et al., 2010). In our study, we took advantage of a unique long-term behavioural and breeding success survey of a breeding population of common goldeneye (Clark et al., 2014; Milonoff et al., 2004; Paasivaara et al., 2010). The common goldeneye is a cavity-nesting diving duck (Cramp & Simmons, 1988; Eadie et al., 1995). The breeding range includes mostly the boreal forests of northern Europe, Asia and North America. More than 80% of the European population breeds in Finland and Sweden (Hagemeijer & Blair, 1997). They often start breeding at 2—3 years of age with the female being the solo incubating sex (Eadie et al., 1995; Milonoff et al., 2002).

By simulating predation-like events, we aimed to investigate the relationship between nest defence behaviour and age/breeding experience. As suggested by previous research (e.g. Gosling, 2001; Urszán et al., 2018), we hypothesized that previous exposure to predation threat affects the individual's response throughout its breeding life span. Either because individuals gain experience by surviving previous predators or because of ageing and the decline in future reproductive opportunities, we expected a positive correlation between nest persistency and age. Further, we investigated the connection between the observed behaviour and current clutch size. Based on parental investment theory, larger clutches are expected to be linked with increased nest care efforts (Albrecht & Klvaňa, 2004; Tinbergen & Daan, 1990). We expected to see individuals with a stronger antipredator response (i.e. bolder) in nests with larger clutches. On the other hand, because larger clutches typically include parasitic eggs (e.g. Pöysä et al., 2001; Eadie et al., 2010), the relationship between female response and clutch size may not be straightforward and could be nonlinear in nature. Indeed, the behaviour of the host female against potential parasites may affect final clutch size; for example, shy females may be more vulnerable to parasitism than bold females, in which case we may expect that individuals with weaker antipredator responses are associated with larger clutches. Finally, we investigated the benefit of exhibiting specific behaviours on hatching success. We anticipated that there would be selection pressure favouring individuals that enhance their fitness against predation. Consequently, we expected to see an association between the direction of the changes in the behaviour of individuals and their overall hatching success. By answering these questions, we aimed to shed light on changes in antipredator behaviour over a longitudinal timescale and its relationship to individuals' reproduction prospects. This understanding will contribute valuable insights into the adaptive nature of nest defence strategies and illuminate the underlying mechanisms driving behavioural variation within populations.

METHODS

Study Population

The study population is located in Maaninka, Finland (Fig. 1). Altogether 484 nestboxes were monitored by Pentti Runko (P.R.) from 1984 to 2021. Incubating females were captured once a year at the end of incubation. A total of 652 females were captured and marked with metal rings. All behavioural, clutch size and female body condition parameters were recorded by P.R. to prevent between-observer bias.

Simulation of Predation Event

During the regular nestbox monitoring procedure, especially during the incubation period, the bird ringer (P.R. in all cases) approached the nestbox. The incubation period for goldeneye lasts for 27–33 days and females typically lay 8–10 eggs (Milonoff et al., 2002; Zicus et al., 1995). Behavioural data were gathered during the incubation stage (usually two or three visits per nest and season) when the female was present at the nest. Many females bred repeatedly in the study area, leading to a mean ±SE of 5.80 ± 0.06 behavioural records per individual per breeding life span. The stage of incubation was assessed by the egg floating method (Liebezeit et al., 2007) during the prehatch visits to the nestboxes, thus allowing a precise estimation of the date and time of hatching. The female was captured and marked and the body condition was measured during the last visit prior to hatching or at hatching time. Since common goldeneye incubate inside nestboxes, their flush response is usually studied differently than for ground-nesting birds. For instance, Mallory et al. (1998) used a distance scoring scale depending on how close the intruder could get to the nest (when approaching the tree, standing under the nestbox, climbing the tree and when opening the nestbox) before initiating a flush response. Similarly in our study, the observer's approach was categorized into three classes based on the distance at which the female reacted to the danger: (1) a 'shy' female left the nest before the ringer approached the nest, or on the capture occasion, she flew into the net when the net was placed in front of the nest's entrance; (2) 'average': female left the nest when the ringer scratched the nestbox wall; (3) 'bold': female left the nest only once physically touched inside the nest or she had to be lifted out of the nestbox.

In cases with multiple visits to the nest, P.R. evaluated the females' behaviour based on their overall performance on multiple visits. If there was no consistent pattern (not being consistent in behaving as shy, average or bold), the individual was categorized as 'average' to be as conservative as possible. All the behavioural records were made by P.R. to prevent observer bias.

Clutch Size and Hatching Success

Clutch size, defined as the number of eggs per nest, was determined when we captured the female. A last visit to the nest was

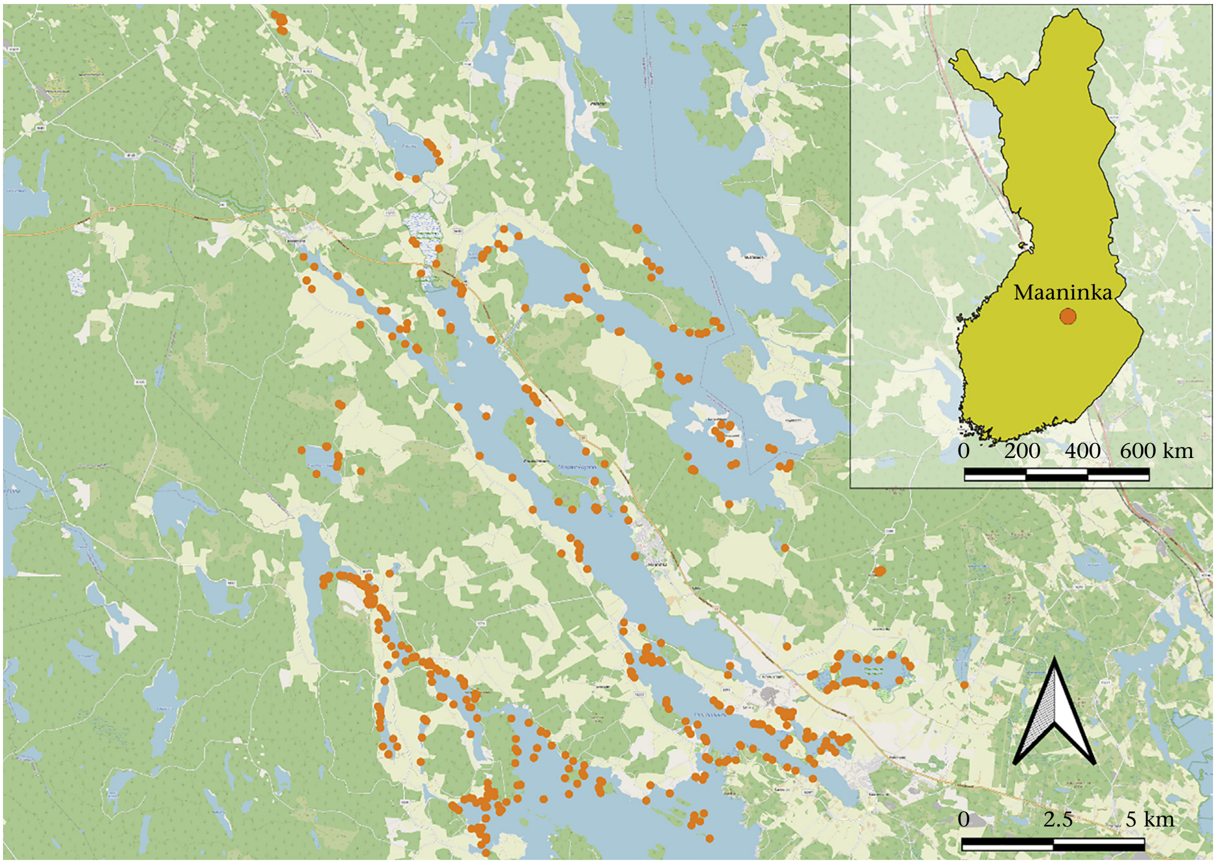

Figure 1. Map of the study area: Maaninka, Finland. Orange circles represent nestbox locations.

made on the hatching day, determined by egg flotation, to ring the ducklings. Ducklings leave the nest within 24 h posthatching (Eadie et al., 1995). During this visit, the hatched eggs and live ducklings were counted. Initially, we calculated the hatching success of a female as the percentage of eggs hatched from the initial clutch size. The data were zero inflated, that is, in many nests all the eggs hatched and there were many failed nests with no hatchlings; for statistical purposes, we divided the data into hatch-success and hatch-failure variables, the former variable containing the number of hatched eggs within the clutch and the latter the number of failed eggs.

Body Condition

Upon capture, females were weighed (with a spring scale to the nearest 1 g), and wing length was measured with a wing ruler to the nearest 1 mm. The body condition of individuals was calculated by dividing their weight by wing length (Schamber et al., 2009).

Brood Parasitism

In common goldeneye, most clutches with 10 or more eggs and practically all clutches with more than 12 eggs are parasitized (Pöysä et al., 2001; Eadie et al., 2010). To study the relationship between CBP and host female behaviour, we considered clutches containing 13 eggs and more (11.20% of all nests, $N = 259$ of 2312) as parasitized nests.

Age Determination of Individuals

Females were at least 2 years of age when first recruited into the breeding colony. The age was calculated based on the hatching year of the individual (Milonoff et al., 2002). Then, if the female was ringed as a duckling, we could tell her age by counting from her hatching date (e.g. 2 years old: in the second year after the hatching year; 3 years old: in the third year after the hatching year, etc.). Otherwise, if the individual was new in the population and was not ringed as a duckling, the hatching year was unknown and thus the age determination was based on the moult sequencing of the feathers. In this case, the age was calculated based on the estimated hatching year (e.g. 2 years old: at least in the second year after hatching; 3 years old: at least in the third year after the hatching year, etc.). After the first breeding attempt in the area, the individual was ringed and thus their age could be followed in future breeding seasons.

Ethical Note

All the behavioural data in our study were collected as part of the regular nest monitoring activities conducted by P.R., ringing licence 863, issued by the Finnish Museum of Natural History (LUOMUS) ringing centre. The nestbox design was developed over time based on experience of which features provided a safe and warm nesting cavity. The latest design is 60 cm in height, with a double floor (inner and outer) and a movable roof. The entry hole has a diameter of approximately 105 mm, positioned 20 cm below the roof's apex. In addition, a 10 cm thick layer of slightly compressed wood chips was added to the bottom of the nest to mimic the rotten wood in natural cavities. Bird monitoring was carried out to induce the least possible stress to the birds. For that reason, most of the visits (77.68%) were in the second half of incubation to minimize the risk of nest abandonment by females. Except for the capture day, at the end of incubation, the study individuals were not physically manipulated on any other occasion. The weighing scale and ruler were disinfected between nest visits to reduce the chance of contamination transfer between individuals. We confirm that our research complies with the ASAB/ABS Guidelines on the use of Animals in Research.

Statistical Analyses

All analyses were conducted using R (version 4.4.0; R Core Team, 2024). We investigated the effect of age, clutch size and body condition on behaviour and, later, they were also accounted for while modelling the effect of behaviour on hatching success. Because nest parasitism and clutch size were correlated ($r_s = 0.55$, $P < 0.05$), we included only clutch size in the analyses. Correlations between age and clutch size, age and body condition and body condition and clutch size were low ($0.12 \leq r_s \leq 0.22$); thus, these variables were included in the same models, as correlation coefficients between predictor variables of $|r| < 0.7$ are generally considered acceptable to avoid problems due to collinearity (Dormann et al., 2013).

Initially, we investigated the effect of age and clutch size change on the behavioural type of individuals using a cumulative linked mixed model (CLMM) from the 'ordinal' package (Christensen, 2022). The model consisted of age, clutch size, body condition, and the interaction between age and clutch size as independent variables. We anticipated a nonlinear relationship between clutch size and behaviour, specifically when combined with the interactive effect of age. Thus, we also added a quadratic term for clutch size in our model to account for a possible nonlinear change in behaviour with clutch size. The individual bird's ID was included as a random effect to account for between-individual differences in behaviour and the fact that the behavioural response of many females was recorded several times over the study period. For significant effects, we carried out an estimated marginal means (emmeans) to examine the differences between age groups and clutch sizes (Russell, 2023).

To complement the model output, we conducted an analysis of repeatability on a subset of data with females breeding at least twice in the population to explore how much of the variance in behaviour was attributable to between-individual difference (examples of within-individual variation in behaviour across years are given in the Supplementary material). We calculated the intraclass coefficient by dividing the variance component of individuals by the total variance of random intercept, plus residual variance (ICC; Nakagawa & Schielzeth, 2010). Then, using a behavioural reaction norm approach, we carried out a mean-centring method (Dingemanse et al., 2010; Mohring et al., 2022; van de Pol & Wright, 2009). We separated the contribution of within-individual and between-individual changes in age and clutch size on behaviour. The between-individual component was the mean of all records for each individual and the within-individual value was calculated by subtracting each individual record from the individual mean. Hence, we were able to consider individual and population level change in behaviour.

To explore whether the behaviour affected the hatching success of individuals, we employed a beta-regression approach with zero inflation, due to the abundance of 100% and 0% values (Ospina & Ferrari, 2012). We divided the hatching success data into hatch-success and hatch-failure, the former including the number of hatched eggs within the clutch and the latter, the number of unhatched eggs in the clutch. Goodness of fit of a model was compared with simpler models and null models using the corresponding Akaike information criterion (AIC), likelihood ratio test (LRT) as well as residual testing via the 'DHARMa' package (Hartig & Lohse, 2022; Table 1). Plots were generated using the 'ggplot2' (Wickham, 2016) and 'graphics' packages (R Core Team, 2024).

Table 1
Description of the data set, the overall number of behavioural observations and females breeding in the area as well as their age and clutch size ranges

	N	Range	Mean ±SE
Number of monitored nests	450		
Number of unique female IDs	652		
Number of behavioural records	2312		
Number of parasitized nests ($n \geq 13$ eggs)	259		
Age range of individuals		2–17	5.35 ±0.06
Breeding attempt frequency range		1–15	5.80 ±0.06
Clutch size range		1–19	9.01 ± 0.05
Wing length range (mm)		185–218	200.79± 0.09
Weight range (g)		467–716	594.84± 0.69

RESULTS

In total, 652 different females were captured, and 2312 behavioural responses were documented of which 522 (22.57% of 2312) were based on one flush response during the incubation period. For 77.42% of all the records ($N = 1790$ of 2312), female behaviour was recorded on multiple occasions during incubation as part of the nestbox monitoring. It is noteworthy that 77.68% of all the visits to the nests in our data set were performed within the last 15 days of incubation; hence we anticipated that this would standardize the impact of incubation stage on our measure of antipredator behaviour (Mallory et al., 1998).

The age of the females when their behaviour was recorded ranged from 2 to 17 years (Table 1, mean ±SE = 5.35 ±0.06), with 34.16% observations ($N = 790$ of 2312) from females between 2 and 3 years old. Of the 652 captured individuals, 448 bred in the area for at least 2–15 years. The body condition index ranged from 2.28 to 3.63 (mean ±SE = 2.96 ± 0.003). Clutch sizes varied from one to 19 (mean ±SE = 9.01 ± 0.05), with 11.20% ($N = 259$ of 2312) containing 13 eggs and more, and thus considered parasitized nests. Among all the nests 43.07% ($N = 996$ of 2312) had a 100% hatching success rate, that is, the whole clutch hatched.

Overall, bold behaviour was less frequent ($N = 397$) than shy behaviour ($N = 990$; $\chi^2_1 = 92.32$, $P < 0.001$) and average behaviour ($N = 925$; $\chi^2_1 = 47.65$, $P < 0.001$). Table 2 shows the models used for the analysis.

Effect of Age of Breeding Females

First, we looked at the distribution of behavioural types in each breeding age (Fig. 2). The percentage of individuals expressing each behavioural type varied significantly across age groups ($\chi^2 = 11.148$, $P = 0.003$). For example, the percentage of shy females tended to decline from 0.48% among 3-year-old breeders to 0.38% among 8-year-old females ($\chi^2 = 3.758$, $P = 0.052$), whereas that of bold females increased from 13% of 3-year-old breeders to 25% among 8-year-old females ($\chi^2 = 10.727$, $P = 0.001$).

Based on the CLMM1, the behaviour of individual females changed in relation to their age (breeding experience; Fig. 3a; estimate± SE = 0.219± 0.058, $Z = 3.749$, $P < 0.001$). Estimating the average response of individuals, using the emmeans package (Appendix, Table A1) revealed that at the age of 2, the probability of finding bold individuals (8%) was significantly lower than finding shy (44%) and average birds (48%). As females aged and gained more breeding experience, there was a noticeable decline in the probability of observing shy individuals within the population such that by the age of 10, the probability of encountering a bold female increased to 15%, while the probability of finding a shy individual declined to 27%. At this point, the difference between bold and shy types was nonsignificant, and both were significantly lower than average types (58%). Finally, for birds at 15 years of age, the probability of finding a bold individual within the population exceeded the probability of observing a shy individual, reaching over 22%, higher, although not significantly, relative to that of shy individuals (19%). The average type (59%) maintained its significantly higher probability compared to shy and bold individuals.

Effect of Clutch Size and Nest Parasitism

There was a strong link between the behavioural type and clutch size (Fig. 3b; estimate± SE = 0.336± 0.103, $Z = 3.256$, $P < 0.01$). Emmeans analysis (Appendix, Table A2) showed that for a small clutch of two, females were significantly less likely to exhibit boldness (4%) than shy (62%) and average behaviour (34%). As clutch size increased, the likelihood of bold type behaviour increased whereas that of shyness declined. At a clutch size of eight, the probability of finding a bold female in the nest increased to 10%, whereas the probability of shyness dropped to 39%. Within the same clutch size, the probability of exhibiting average behaviour

Table 2
Selected models for the statistical analyses

Model	Response variable	Independent variable(s)	Random effect	Goodness of fit
CLMM1	Behaviour	~ Age * ClutchSize+ Body.condition+ I(ClutchSize^2)	FemaleID	AIC: 4317.987 LogLik: 2150.993
CLMM2	Behaviour	Age * ClutchSize + Body.condition	FemaleID	AIC: 4320.422 LogLik: 2152.211
CLMM3	Behaviour	Age + ClutchSize + Body.condition	FemaleID	AIC: 4325.513 LogLik: 2155.757
CLMM.NULL	Behaviour	~ 1	FemaleID	AIC: 4361.263 LogLik: 2177.631
Beta1 (ziformula = ~1)	cbind (hatchSuccess, hatchFailure)	~ Behaviour + poly (Age,2) + poly (ClutchSize,2)+Body.condition	FemaleID	AIC: 6966.127 LogLik: 3472.063 DHARMa residual dispersion = 1.0151, $P > 05$
GLMMTMB.NULL	cbind (hatchSuccess, hatchFailure)	~ 1	FemaleID	AIC: 7065.570 LogLik: 3528.785
Beta2 (GLMMTMB not zero-inflated term)	cbind (hatchSuccess, hatchFailure)	~ Behaviour + poly (Age,2) + poly (ClutchSize,2)+Body.condition	FemaleID	AIC: 7689.819 LogLik: 3834.909
Beta3 (GLMMTMB simple)	cbind (hatchSuccess, hatchFailure)	Behaviour + Age + ClutchSize + Body.condition	FemaleID	AIC: 7697.307 LogLik: 3840.653

The CLMM and GLMMTMB models were compared with associated alternative models as well as the null model using AIC and logLik comparison. The fit of the chosen beta-regression model (Beta1) was further evaluated via a DHARMa residual test.

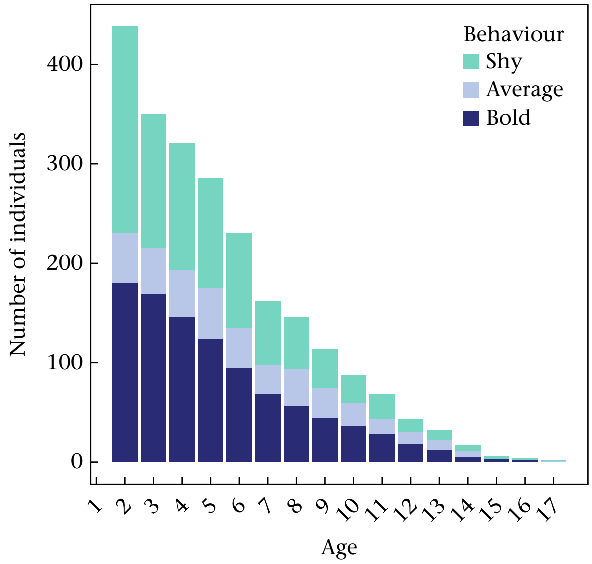

Figure 2. Frequency of breeding common goldeneye females belonging to one of three behavioural types, shy, average and bold, in relation to their estimated age.

(51%) was nonsignificantly higher than the probability of showing shyness and significantly more than the probability of showing boldness. Among larger clutch sizes, the same trend persisted.

On the other hand, the model also supported the inclusion of a quadratic relationship between clutch size and behaviour (estimate± $\mathrm{SE} = -0.010 \pm 0.005$ $Z = -1.984$, $P < 0.05$). The slope of the increase in boldness probability with clutch size declined for clutches over 12 (the parasitism threshold). When the clutch reached 13, the probability of boldness behaviour was slightly higher at 12%. The probability of finding a shy individual in the nest declined to 33%, although it remained significantly higher than the probability of finding a bold female. Again, females were more likely to exhibit average behaviour (55%) than boldness or shyness. Subsequently, in a clutch of 15 eggs, the probability of bold behaviour in females further declined to 11% whereas the probability of shy behaviour increased to 34% (average type probability showed less difference and remained at 55%).

Repeatability and Within- and Between-Individual Coefficients

We found a relatively high rate of repeatability in between-individual differences ($R = 0.46$), indicating that 46% of total variance in behaviour was due to the between-individual differences in behaviour.

Further, behaviour was affected by females' age at the individual level (within-individual coefficient estimate± $\mathrm{SE} = 0.119 \pm 0.021$, $Z = 5.650$, $P < 0.001$), whereas the between-individual contribution of differences in age on behaviour was not significant (mean-age coefficient estimate± $\mathrm{SE} = -0.012 \pm 0.049$, $Z = -0.258$, $P > 0.05$). Similarly, within-individual increase in clutch size led to increased probability of bold behaviour (within-individual coefficient estimate± $\mathrm{SE} = 0.288$, $Z = 0.120$, $P < 0.05$), while differences in clutch size between individuals did not have a significant effect on the probability of behaviour (mean-clutch size coefficient estimate± $\mathrm{SE} = 0.225 \pm 0.129$, $Z = 1.732$, $P > 0.05$). Overall, the mean-centring approach confirmed the validity of the CLMM1 model in terms of the effect of change at the individual level on behaviour.

Interaction Effect of Age and Clutch Size

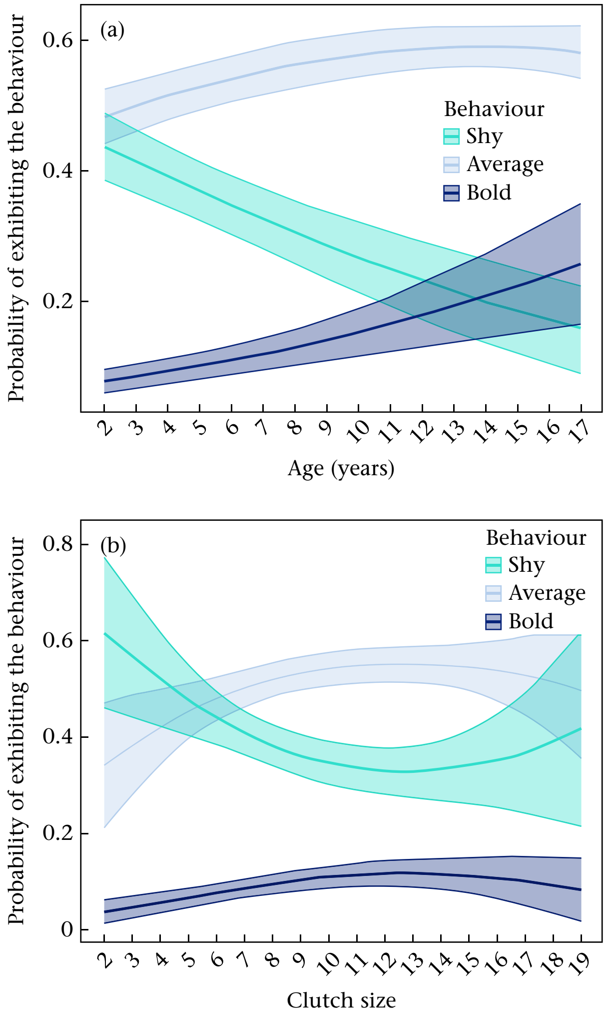

Figure 3. Probability of a breeding common goldeneye female exhibiting one of three behavioural types in relation to (a) age/breeding experience and (b) clutch size. The graphs are derived from the emmeans analyses of the CLMM1 (Table 2). Individual IDs were included in the model to account for between-individual variation. Shaded areas represent 95% confidence intervals, indicating the plausible values for the population level trend of behaviour.

A significant interaction between age and clutch size was observed in relation to behaviour (Fig. 4; estimate± $\mathrm{SE} = -0.013 \pm 0.006$, $Z = -2.243$, $P < 0.05$). Among the 2-year-old nesters, with a small clutch of two eggs, the probability of bold behaviour (2%) was significantly lower than in shy (76%) and average individuals (22%; Appendix, Table A3). Keeping clutch size fixed, the probability of encountering a bold individual increased with age, whereas shy nesters became less frequent. However, although still increasing, when clutch sizes exceeded 10 eggs, which also included parasitized nests, the slope of the age-dependent increase in boldness was lessened. With a clutch size of 13 eggs (one parasitic egg), the probability of being bold increased from 10% at age 2 (significantly lower than that of shy and average) to 16% at age 15, while the probability of being shy declined from 35% at age 2 to 25% at 15 (nonsignificantly larger than the bold probability). The average behaviour probability increased slightly from 53% at age 2 to 58% at 15.

Finally, in the largest clutches (19 eggs), the probability of finding a bold female declined with age (from 10% at age 2 to 5% at age 15). On the other hand, the probability of finding a shy female in a nest with 19 eggs increased from 38% at age 2 to 53% at age 15. Average behaviour also declined slightly from 52% at age 5 to 42% at age 15.

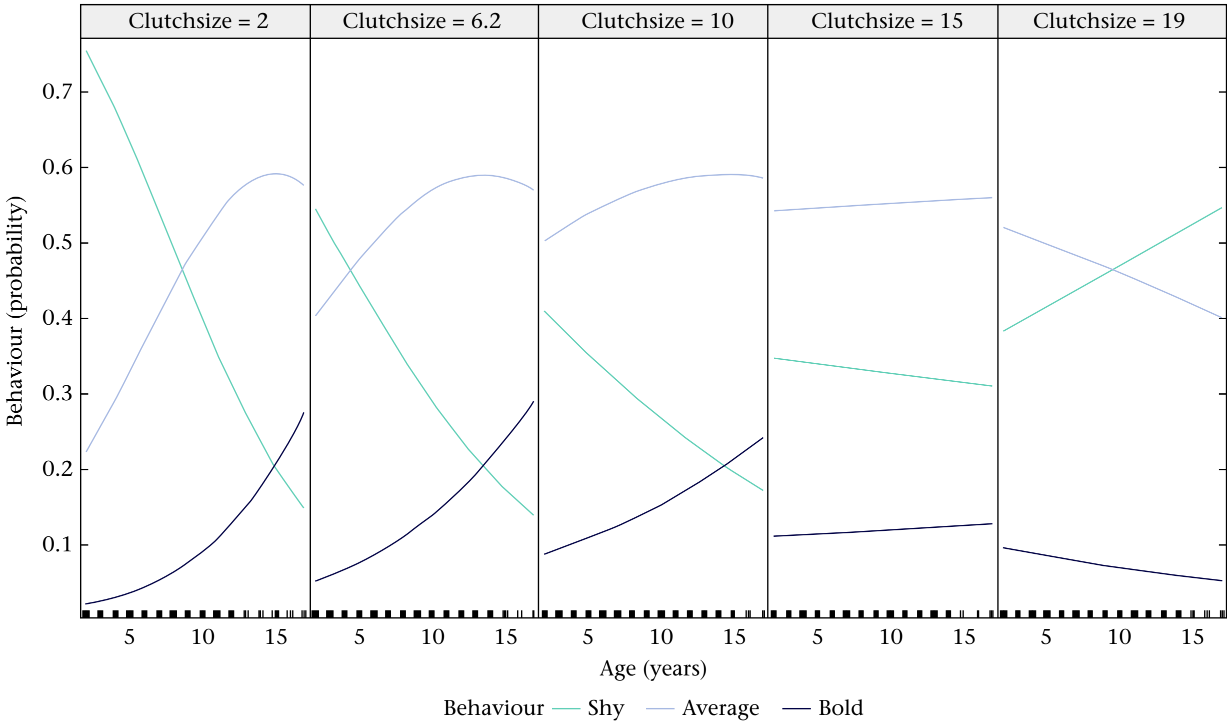

Figure 4. Probability of a breeding common goldeneye female exhibiting one of three behavioural types in association with the interaction effect of age and clutch size. The plot is derived from the CLMM1model (Table 2) and contains the random effect of individual ID to control for the within-individual interaction. The vertical bars represent 95% confidence intervals. The width of the bars indicates the uncertainty in the estimated probability, with narrower bars suggesting higher precision in the estimates.

Hatching Success

The zero-inflated beta regression model did not reveal any significant effect of behaviour on hatching success (shy type and hatching success: estimate ± SE = 0.024± 0.066, $Z = 0.360$, $P > 0.05$; bold type and hatching success: estimate ± SE = 0.039± 0.087, $Z = 0.466$, $P > 0.05$; average type and hatching success: estimate ± SE = −0.024± 0.066, $Z = -0.361$, $P > 0.05$).

DISCUSSION

Our study revealed that the antipredator response of incubating common goldeneye females to nest disturbance was correlated positively with female age (breeding experience). There was a nonlinear probability of a female expressing bold behaviour in relation to clutch size (concave; i.e. positively increasing and then decreasing around the parasitism threshold). Conversely, the probability of females exhibiting shy behaviour tended to increase with the number of parasitic eggs in the nest. Surprisingly, we found no evidence that female behaviour was related to hatching success.

Unlike Mallory et al. (1998), who found no significant relationship between nest defence of common goldeneye and clutch size, our study indicated a significant relationship between clutch size and female nest defence. However, interpreting the relationship between clutch size and nest defence was complicated by an interaction between age and clutch size, and the effects of conspecific brood parasitism (CBP). A closer examination of the pattern of the relationship between female nest defence and clutch size, particularly the interaction between clutch size and female age, provided important new information concerning the role of host female nest defence behaviour in CBP. In principle, the propensity to defend the nest against parasites could be reflected in the behaviour of the females. The probability of females showing bold behaviour increased with clutch size only up to the parasitism threshold (12 eggs per clutch). When the interaction between clutch size and female age was considered, the probability of occurrence of the bold type decreased with age especially for heavily parasitized clutches, whereas that of the shy type increased. One interpretation of these patterns could be that nests of shy and old females were more prone to get parasitized than nests of bold and old females. Further research, preferably experimental, is needed to confirm these intriguing new findings.

Our results are consistent with life history trade-off models, suggesting that individuals with higher potential future reproductive opportunities will be more likely to avoid a threat whereas those with lower future reproductive prospects would invest more in the current breeding effort (Patrick et al., 2013). There is increasing evidence that birds are able to assess and change their future breeding performance throughout ecological time (Lima, 2009; Touati et al., 2023). For example, Touati et al. (2023) showed that older white storks, *Ciconia ciconia*, had shorter flight initiation distance (FID) responses (flushed from nests at a shorter distance from an intruder). These scenarios predict that the cost of fleeing from a perceived predation threat is an investment weighted against the subsequent fitness advantage (Nonacs & Blumstein, 2010), that is, older individuals are predicted to value current reproduction over future opportunities, as exhibited by their tendency to flush later.

The age-dependent increase in boldness levels of individuals could also be a result of their perception of the predation risk; for example, stronger antipredator responses are observed in perch, *Perca fluviatilis*, with previous exposure to predators, as well as for those in high-risk populations (Magnhagen & Borcherding, 2008). On the other hand, survival experience from a prior perceived predation risk might affect the future behaviour, allowing the individual to breed more confidently. For example, shy minnows, *Pimephales promelas*, became bolder after winning a fight (Frost et al., 2006).

One limitation of our study was that we were not able to evaluate the impact of the previous year's exposure to human approach on the risk perception of females, although it is possible that females gain experience in distinguishing between humans and a real predator and/or habituate to a repeated perceived risk. However, we believe that the underlying economics of the antipredator behaviour persists, that is, a female must change her attention/energy use during incubating in response to the trade-offs of self-survival (future reproduction) versus the current reproductive effort (Frid & Dill, 2002). Note that, because the females studied here bred in nestboxes, they did not have direct contact with the intruder, minimizing possible habituation to human disturbance. Another limitation of our study could be that we cannot ignore the possibility that some individuals might change their behaviour during the last 15 days (the period when most of our observations occurred) which was not directly reflected in our behavioural categories. Still, given the limitation of checking a huge number of nests at the same time each year and considering the number of monitored individuals, we assume that the interannual behavioural trend reliably reflects the change in behaviour mainly due to the female ageing/gaining breeding experience, rather than the variation in the timing of gathering the behavioural data. In our study, despite the plasticity of behaviour at the individual level, there were also consistent differences between females. Adding to that, some individuals had a fixed behavioural type over the years (see Supplementary Fig. S1), suggesting a lack of significant dominance of one behavioural type over the others in terms of hatching success.

By incorporating a large longitudinal data set and by separating the contribution of within- and between-individual changes in age and clutch size on behaviour, we were able to unfold an interesting aspect of antipredator behaviour based on an individual's state, notably age. That the between-individual component of age did not significantly affect the behaviour suggests that the increased probability of females showing boldness in our model is primarily due to the plastic change in individual females' behaviour over their life span and not selective disappearance of shy females over the years (see also de Jong et al., 2021) as might be suggested by the change in the proportion of behavioural types with age. In other words, the significant behavioural plasticity of individuals over time (age) was reflected in the shifting proportions of behavioural types, with a higher proportion of bold females and lower proportion of shy females among the older age groups. Still, we cannot rule out the possibility of higher survival and/or higher continued breeding of bold individuals also influencing the population level probability of bold/shy behaviour. On the other hand, the high repeatability of behaviour within individuals does suggest that different behavioural types coexist within our population. Why might these differences in nest defence behaviour coexist and what maintains the variation? From a personality point of view, traits (e.g. boldness and aggression) are often correlated across contexts, meaning that exhibiting one predicts the occurrence of another (Dingemanse et al., 2012; Patrick et al., 2017; Wolf et al., 2007). It is feasible that being shy or bold is correlated with several activities which cumulatively affect individual fitness. In great tits, *Parus major*, shy individuals invest more in survival than reproduction compared with bold breeders (Cole & Quinn, 2014). In a review, exploring the adaptive perspective of personality, Wolf et al. (2007) suggested that, based on the trade-off between current and future reproduction opportunities, coexistence of different behavioural types within populations is predicted by life history theory. Conceivably, when an incubating common goldeneye female is young (with a high prospect of future breeding), she might maximize her own survival by flushing sooner when perceiving a predation danger and invest more time in foraging (shy individuals might also expected to be more explorative, Wolf et al., 2007). As the female gets older, the focus shifts towards investing energy in clutch production and increasing nest care persistence to maximize the brood's survival, that is, she becomes bolder.

Some studies (e.g., Sinn et al., 2008) suggest that predation-induced selection might not directly act on shyness/boldness types but the fitness trade-offs across different developmental stages affect the selection trajectory. In a meta-analysis on fitness consequences of personality, Smith and Blumstein (2008) pointed out that the trade-off between the reproductive success of bolder individuals and survival costs results in conserved variation in boldness levels among individuals. Moreover, as illuminated by Dingemanse et al. (2004), depending on the annual condition of the habitat (e.g. availability of food and predators), selection might act in a fluctuating manner, resulting in habitat-dependent maintenance of the behavioural types along the shy—bold continuum.

Interestingly, despite the plastic nature of behaviour at the individual level, along with a high level of consistent behavioural differences between individuals, none of the behavioural profiles of incubating females studied here demonstrated an advantage in terms of hatching success. This indicates that antipredator behaviour alone might not directly predict reproductive success. Given the complexity of predicting a longitudinal antipredator response and its fitness consequences in wildlife, we encourage experimental studies focusing on the plasticity of an antipredator response with age while controlling for the homogeneity of other environmental factors.

Author Contributions

Céline Arzel: Writing – review & editing, Supervision. **Farshad S. Vakili:** Writing – review & editing, Writing – original draft, Software, Funding acquisition, Formal analysis, Conceptualization. **Hannu Pöysä:** Writing – review & editing, Data curation, Conceptualization. **Océane Liehrmann:** Writing – review & editing, Formal analysis. **Pentti Runko:** Methodology, Investigation, Data curation. **Stefan Björkman:** Writing – review & editing, Supervision.

Data Availability

The data set used for this study is available at https://doi.org/10.23729/62ad1417-dcaf-4224-83b5-cb51605ca4a6. The code script is accessible via https://github.com/FarshadSV/Goldeneye.git.

Declaration of Interest

The authors report that there are no personal or economic conflicts of interest.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2024.12.002.

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Appendix

Table A1

Significant differences between the behavioural types (shy, average and bold) observed in breeding common goldeneye based on age

Interpretation	Age (years)	Probability (%)			Significance
		Shy	Average	Bold	
Emmeans	2	44	48	8	Bold ~Shy: estimate± SE = 0.35± 0.03, $Z = 10.550$, $P < 0.001$ Bold ~ Average: estimate± SE = 0.40± 0.01, $Z = 21.737$, $P < 0.001$
Emmeans	10	27	58	15	Bold ~Shy: estimate± SE = 0.11± 0.04, $Z = 2.62$, $P < 0.05$ Bold ~ Average: estimate± SE = 0.42± 0.02, $Z = 18.562$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.31± 0.04, $Z = -7.449$, $P < 0.001$
Emmeans	15	19	59	22	Bold ~Shy: estimate± SE = −0.38± 0.06, $Z = -0.56$, $P > 0.05$ Bold ~ Average: estimate± SE = 0.36± 0.04, $Z = 7.779$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.40± 0.03, $Z = -11.325$, $P < 0.001$

Table A2

Significant differences between the behavioural types (shy, average and bold) observed in breeding common goldeneye based on clutch size

Interpretation	Clutch size	Probability (%)			Significance
		Shy	Average	Bold	
Emmeans	2	62	34	4	Bold ~Shy: estimate± SE = 0.58± 0.09, $Z = 6.31$, $P < 0.001$ Bold ~ Average: estimate± SE = 0.30± 0.05, $Z = 5.54$, $P < 0.001$
Emmeans	8	39	51	10	Bold ~Shy: estimate± SE = 0.28± 0.02, $Z = 9.833$, $P < 0.001$ Bold ~ Average: estimate± SE = 0.42± 0.01, $Z = 22.912$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.13± 0.03, $Z = 3.518$, $P < 0.01$
Emmeans	13	33	55	12	Bold ~Shy: estimate± SE = 0.20± 0.03, $Z = 5.514$, $P < 0.001$ *Bold ~ Average:* estimate± SE = 0.43± 0.01, $Z = 21.968$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.22± 0.04, $Z = -5.059$, $P < 0.001$
Emmeans	15	34	55	11	Bold ~Shy: estimate± SE = 0.22± 0.05, $Z = 4.110$, $P < 0.001$ Bold ~ Average: estimate± SE = 0.43± 0.01, $Z = 21.927$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.20± 0.06, $Z =$ - 3.348, $P < 0.001$

Table A3
Major findings on the differences between the behavioural types (shy, average and bold) observed in breeding common goldeneye based on the interaction between age and clutch size

Interpretation	Clutch size	Age (years)	Probability (%)			Significance
			Shy	Average	Bold	
Emmeans	2	2	76	22	2	Bold ~Shy: estimate± SE = 0.73± 06, $Z = 10.726$, $P < 0.001$ Bold ~ Average: estimate± SE = 0.20± 0.04, $Z = 4.232$, $P < 0.001$ Average ~ Shy: estimate± SE = 0.53± 0.11, $Z = 4.572$, $P < 0.001$
Emmeans	2	10	40	51	9	Bold ~Shy: estimate± SE = 0.30± 0.14, $Z = 2.162$ $P > 0.05$ Bold ~ Average: estimate± SE = 0.41± 0.03, $Z = 11.081$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.11± 0.17, $Z = -0.621$, $P > 0.05$
Emmeans	6	2	55	40	5	Bold ~Shy: estimate± SE = 0.50±0.03, $Z = 13.620$, $P < 0.001$ Bold ~ Average: estimate± SE = 0.34± 0.02, $Z = 16.034$, $P < 0.001$ Average ~ Shy: estimate± SE = 0.15± 0.05, $Z = 2.812$, $P < 0.05$
Emmeans	6	15	17	59	24	Bold ~Shy: estimate± SE = −0.06 ± 0.09, $Z = -0.65$, $P > 0.05$ Bold ~ Average: estimate± SE = 0.34 ± 0.06, $Z = 5.09$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.41± 0.03, $Z = -10.481$, $P < 0.001$
Emmeans	10	2	35	54	11	Bold ~Shy: estimate± SE = 0.24 ± 0.03, $Z = 7.745$, $P < 0.001$ Bold ~ Average: estimate± SE = 0.43 ± 0.01, $Z = 22.563$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.18± 0.03, $Z = -4.651$, $P < 0.001$
Emmeans	10	15	20	59	21	Bold ~Shy: estimate± SE = −0.01 ± 0.07, $Z = -0.248$, $P > 0.05$ Bold ~ Average: estimate± SE = 0.37 ± 0.04, $Z = 8.388$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.39± 0.03, $Z = -9.892$, $P < 0.001$
Emmeans	13	2	36	54	10	Bold ~Shy: estimate± SE = −0.25 ± 0.05, $Z = 4.726$, $P < 0.001$ Bold ~ Average: estimate± SE = 0.42 ± 0.01, $Z = 21.790$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.17± 0.06, $Z = -2.842$, $P < 0.05$
Emmeans	13	15	25	59	16	Bold ~Shy: estimate± SE = 0.08 ± 0.10, $Z = 0.844$, $P > 0.05$ Bold ~ Average: estimate± SE = 0.41 ± 0.03, $Z = 12.071$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.33± 0.07, $Z = -4.228$, $P < 0.001$
Emmeans	15	2	35	54	11	Bold ~Shy: estimate± SE = 0.23 ± 0.07, $Z = 3.048$, $P < 0.01$ Bold ~ Average: estimate± SE = 0.43 ± 0.02, $Z = 21.171$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.19 ± 0.08, $Z = -2.229$, $P > 0.05$
Emmeans	15	15	32	56	12	Bold ~Shy: estimate± SE = 0.18 ± 0.13, $Z = 1.427$, $P > 0.05$ Bold ~ Average: estimate± SE = 0.43 ± 0.02, $Z = 21.519$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.24 ± 0.13, $Z = -1.831$, $P > 0.05$
Emmeans	19	2	38	52	10	Bold ~Shy: estimate± SE = 0.28 ± 0.16, $Z = 1.691$, $P > 0.05$ Bold ~ Average: estimate± SE = 0.42 ± 0.03, $Z = 11.296$, $P < 0.001$ Average ~ Shy: estimate± SE = −0.13 ± 0.20, $Z = -0.672$, $P > 0.05$
Emmeanse	19	15	53	42	5	Bold ~Shy: estimate± SE = 0.46 ± 0.20, $Z = 0.360$, $P > 0.05$ Bold ~ Average: estimate± SE = 0.36 ± 0.09, $Z = 3.762$, $P < 0.001$ Average ~ Shy: estimate± SE = 0.10 ± 0.29, $Z = 0.360$, $P > 0.05$