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ORIGINAL ARTICLE

Costs of personality: bold incubating goldeneye females risk their lives when a predator attacks

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Abstract Consistent among-individual differences in behavioural traits (animal personality) have been documented in several animal taxa. However, mechanisms driving the evolution and maintenance of such differences in natural populations are still unclear. One widely upheld hypothesis emphasizes trade-offs between survival and reproduction as such a mechanism; e.g., risk-taking individuals often have higher reproductive success but also higher mortality. Hence, a key prediction is that individuals expressing riskier behaviours should suffer greater mortality. Recent reviews have questioned the generality of trade-offs-based explanations of consistent among-individual differences in behavioural traits. A fundamental research gap here is that a direct link between a personality trait and mortality risk has rarely been documented in the wild. We studied risk-taking behaviour (boldness) of incubating common goldeneye (*Bucephala clangula*) females, a hole-nesting precocial avian species. Repeatability of female behaviour along the shy-bold continuum was high within a season: we observed little within-individual variation but consistent differences among females. We found that, among incubating females that faced a nest predator that could kill a female, those females that behaved bold against human-induced disturbance were killed with a high probability. Females that got killed were not exceptional in terms of nesting or in terms of overall predation risk of the nest sites (proportion of depredated nesting attempts in a nestbox) they occupied compared with females in randomly drawn samples from the pooled data of killed and survived females. Hence, our study provides direct evidence of a predation cost of a personality trait (highly repeatable boldness) under natural conditions.

Significance statement
Animal personality traits may affect an individual's survival probability and reproductive success, but a direct link between personality trait and mortality has rarely been documented in the wild. We addressed this shortcoming by studying risk-taking behaviour of incubating common goldeneye females, a hole-nesting avian species. Common goldeneye females face a real mortality risk, because the most important nest predator, the pine marten, can kill females. We recorded the response of females to a human observer approaching the nestbox and scored the behaviour along a shy-bold continuum. We found that among all females that faced a dangerous predator, the boldest females were killed with a high probability. Our study provides evidence that predation risk is an important selection pressure in the evolution and maintenance of among-individual variation in behavioural traits in natural populations.

Keywords Boldness · Personality · Predation risk · Repeatability · Risk-taking · Shy-bold continuum

Introduction

Among-individual variation in behaviour (animal personality) has been recognized important in the evolution of life-history parameters and to have important population and community-level consequences (Wolf and Weissing 2012; Laskowski et al. 2020). How a given personality trait affects individual fitness is crucial for both understanding the evolution of personality traits and to predict their consequences for various ecological processes. Whereas earlier theoretical and empirical

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work emphasized the role of trade-offs between survival and reproduction in explaining consistent among-individual differences in personality in animal populations (Wolf et al. 2007; Biro and Stamps 2008; Smith and Blumstein 2008; see Dingemanse and Wolf 2010; Mathot and Frankenhuis 2018 for comprehensive reviews of models to explain consistent individual behavioural variation), recent meta-analyses and reviews have questioned the generality of this idea (Moiron et al. 2020; Haave-Audet et al. 2022). Contrary to expectations based on life-history trade-offs, empirical studies have often found that behaviours associated with increased survival are also associated with increased reproduction (Moiron et al. 2020; Haave-Audet et al. 2022). A critical shortcoming in the empirical support for the trade-offs-based explanation of personality traits is that direct evidence of survival costs (i.e. observed mortality) of personality traits has rarely been documented in free-living animals (Hulthén et al. 2017).

Boldness, defined by Réale et al. (2007) as an individual's reaction to any risky situation, is an animal personality trait that has been studied extensively in various taxa and systems (Carter et al. 2013; Laskowski et al. 2022). However, even though among-individual variation in risk-taking (boldness) has been demonstrated in numerous studies and several animal taxa (see e.g. Wilson and Godin 2009 and references therein), direct evidence of survival costs even in the context of risk-taking behaviour remains rare. For example, in a recent meta-analysis, Moiron et al. (2020) assessed evidence for the fundamental prediction of theories explaining how among-individual differences in behavioural traits are maintained in animal populations, the specific prediction being that individuals expressing more risky behaviours should suffer greater mortality (see also Réale et al. 2007; Stamps 2007; Biro and Stamps 2008). Based on 27 studies (among which 15 were done in the laboratory and 12 in the field), and using four behavioural types related to risk-taking (exploration, activity, boldness, aggression) and longevity and survival as measures of mortality, Moiron et al. (2020) did not find overall support for the prediction (see also Haave-Audet et al. 2022). Importantly, in only one of the studies done in the wild, the association between risk-taking behaviour and survival was based on explicit records of individual predation events. That study found that bolder individuals of the roach (*Rutilus rutilus*) had a higher risk of being preyed on by cormorants than shy individuals (Hulthén et al. 2017). We are aware of three other studies (not included in the review of Moiron et al. 2020) in which some evidence of a direct link between boldness-related behaviour and mortality risk was provided. Møller (2014) reported for breeding barn swallows (*Hirundo rustica*) that individuals that were found dead due to predation had shorter flight initiation distances at or near the nest than survivors. Santos et al. (2015) studied flocks of homing pigeon (*Columba livia*) and found that individuals more tolerant to human approach, slower to escape from a confined environment and more resistant to human handling were more likely to be preyed on by raptors. Finally, Ward-Fear et al. (2018) found for yellow-spotted monitors (*Varanus panoptes*) that although a lizard's boldness did not make it more or less likely to be killed by a python, boldness affected the timing of mortality due to pythons; bold individuals experienced higher python predation during the wet season, whereas shy individuals were killed primarily in the dry season. While questioning the ability of current theories to explain maintenance of variation in behavioural traits at the among-individual level, Moiron et al. (2020) suggested that one reason for their finding could be that researchers of the original studies probably did not measure truly risky behaviours and/or survival estimates were biased. Clearly, a deeper understanding of conditions under which risky behavioural types would or would not incur a survival cost is needed.

Here, we aim to increase such understanding by studying survival cost of boldness behaviour in incubating common goldeneye (*Bucephala clangula*, hereafter goldeneye) females. Goldeneyes are a hole-nesting species with uniparental female care, i.e. males do not provide female guarding or any parental care after the female has started incubation (Eadie et al. 1995). Hence, incubating goldeneye females provide an excellent model system to study risk-taking behaviour (boldness), because females sitting on eggs cannot rely on males warning of potential danger, nor can they see an approaching intruder but must rely on other cues to assess risks. An earlier study revealed that incubating goldeneye females differ in their boldness behaviour by responding differently to human-induced disturbance (Vakili et al. 2025), a stimulus perceived similarly to predation risk (Frid and Dill 2002). Whereas females typically left the nestbox well before an approaching observer reached it, some females left nestboxes only once physically touched (see Vakili et al. 2025 for details). Such bold behaviour exposes incubating females to a high risk when a nest predator that can kill the female attacks. The main predators of goldeneye clutches, both in natural cavities such as old nest holes of black woodpecker (*Dryocopus martius*) and in nestboxes provided by human, in Europe are the pine marten (*Martes martes*) and the stone marten (*Martes foina*) (Dow and Fredga 1983; Johnsson 1993; Pöysä et al. 1997; Ludwichowski et al. 2002; Sonerud et al. 2023). In some study areas, American mink (*Neogale vison*) prey on goldeneye clutches (HP unpublished). All these mammalian species can kill incubating goldeneye females (hence, hereafter we use the term "predator" instead of "nest predator"). For example, Ludwichowski et al. (2002) mentioned that 12 goldeneye females were killed in their nestbox by martens (*Martes* spp.) and Sonerud et al. (2023) reported that in 8 out of 173 nest depredation cases the goldeneye female had been killed by pine martens. Hence, an obvious question arises: are goldeneye females that will be killed by these predators exceptionally bold? Answering this question addresses an important issue concerning presumed costs of animal personality (Moiron et al. 2020), specifically risk-taking behaviour at a critical stage (reproduction) of avian life cycles. Considering that, despite a lot of research effort, empirical evidence for life-history trade-offs in affecting risk-taking in incubating birds in general is less than compelling (Graham and Shutler 2019), it is surprising that direct empirical evidence even of the link between risk-taking behaviour and mortality risk is almost non-existent.

Here, we address survival costs of personality traits by investigating if bold incubating goldeneye females risk their lives when a predator attacks. To that end, we use a long-term (1992–2024) database on responses of incubating females to human-induced disturbance. This database is unique because it includes also behavioural data for killed females which is typically lacking from other studies on fitness consequences of personality traits (see above). Our focus here was in exploring whether the females that were killed during a predator attack were exceptionally bold along a shy-bold continuum among all females that faced an equally dangerous nest depredation event (i.e. all the studied females faced the risk but only some were killed). Female-specific boldness was measured independently of the predator attack as response to human-induced disturbance as in Vakili et al. (2025). Earlier studies in other species have indicated that clutch size, female experience and condition, as well as nest site-dependent predation risk may affect risk-taking behaviour of incubating females (e.g. Albrecht and Klvaňa 2004; Dassow et al. 2012; Mohring et al. 2022). In goldeneyes, timing of breeding and clutch size are characteristics reflecting female experience and condition (e.g. Eadie 1989; Clark et al. 2014) and predation risk varies among nest sites (Pöysä 1999; Pöysä and Pesonen 2007). Hence, we also studied if the killed females differed in terms of these 3 characteristics from the females that faced an equally dangerous nest predation. Finally, we studied the repeatability of the boldness behaviour in incubating goldeneye females to assess the consistency of among-individual differences in this risky trait.

Materials and methods

Study area and data

The study area in southeastern Finland (61°35 N, 29°40 E) is about 59 km^2 and dominated by pine *Pinus sylvestris* L. or mixed (pine, birch *Betula* spp. and spruce *Picea abies* (L.) Karst) forests interspersed with lakes of varying size and luxuriant, emergent vegetation. The 37 study lakes (mean size 3.5 ha, range 0.05–24.0 ha) are covered by ice during winter and have a relatively stable water level in summer. Pine martens and American minks are the main predators of goldeneye clutches in the study area (Pöysä et al. 1997). There were 14 old nest boxes available in the study area before 1992. In 1992–1994, new nest boxes were erected in three phases, making together 64 nest boxes from 1994 onwards. In 2008, 30 additional nest-boxed were made available, resulting in a total of 94 nest boxes from 2008 onwards; the extent of the study area has remained unchanged since 1994 (see Pöysä and Pöysä 2002; Pöysä 2024). Nesting attempts and success in the boxes have been recorded annually since 1992. All nestboxes were checked frequently (about once a week or once every two weeks) from about mid-April through early June in each year for nesting attempts (at least one egg laid) and to determine the fate of nesting attempts. The frequency of nestbox visits varied depending on the annual status of the nestbox; nestboxes in which a nesting attempt was recorded were visited more frequently during egg laying and incubation phases to get information on final clutch size, occurrence of conspecific brood parasitism and timing of nest predation (see Pöysä 2024, 2025 for more information). Data on the behaviour of incubating goldeneye females were gathered in 1992–2024 during routine nest visits (carried out by HP alone) when approaching the nest (see Table S1 for nest-specific dates of recording female behaviour). Female response to the disturbance induced by the visit were scored along a shy-bold continuum as follows (hereafter, boldness score): 1 = female left the nestbox when the observer was >5 m from the tree to which a nestbox was attached (nesting tree) (very shy female); 2 = female left when the observer was 1–5 m from a nesting tree; 3 = female left when the observer was next to the nesting tree; 4 = female left when the observer set a ladder to lean against the nesting tree and started to climb to the nest; 5 = female stayed in the nestbox when the observer checked that the female was in the box, either through the entrance hole or by opening the roof of the box (very bold female). The date of each behavioural observation was recorded. If there was more than one behavioural record per female within season mean boldness score and mean date was calculated and used in the bootstrap tests as explained below; boldness behaviour of individual females was relatively constant across recording events (see Fig. S1 for examples and Results; detailed information on recordings per female (nest) is given in Table S1 and Table S2). It was not possible to record data blind because our study involved focal animals in the field. Female behaviour was recorded whenever possible and independently of the fate of the nesting attempt. Females were not captured for ringing or handled otherwise during the nest visits when the behaviour was recorded. In an earlier study, based on data from a different goldeneye breeding population, we found that a corresponding but more crude measure of boldness revealed both consistent among-individual variation and within-individual plasticity across years in boldness (a three-level measure: shy, average and bold; Vakili et al. 2025).

As we were interested in whether the boldness behaviour of an incubating female affected her risk of being killed when a predator attacked, we included only depredated nests for which either the pine marten (vast majority of cases) or an American mink was identified as the predator. Due to this prerequisite, two depredated nesting attempts for which we had behavioural data (boldness scores 1 and 5) were left out, the most probable nest predator in these cases being the great spotted woodpecker (*Dendrocopos major*; in the case of egg predation by a bird, there is typically a round hole of varying size in the egg). In cases where incubating females were not killed, we identified the predator as follows. In the case of pine marten, brown hairs were found at entrance holes, typically all eggs taken and probably cached somewhere for the winter period (usually no remains of eaten eggs were found on the ground near the nestbox), fresh goldeneye down was found on the roof of the nestbox and/or on the tree trunk (see also Nilsson et al. 1991; Pöysä et al. 1997). In the case of American mink, typically some eggs were left in the nestbox, but some were eaten on the ground near the nestbox, with a large rectangular hole in the egg, fresh goldeneye down was found on the roof of the nestbox and/or on the tree trunk. Behavioural data were obtained for 74 nesting attempts depredated during incubation for which the female survived (hereafter surviving female data), and for 17 females that were killed by the predator (hereafter killed female data). Female death was confirmed either by finding carcass in the nestbox or in the immediate vicinity of the nest box (10 females) or by observing fresh blood within the nest box and/or at the entrance hole, often together with other marks of fighting (7 females). The 17 killed females bred in 16 different nest boxes and in 11 different years (first observation in 1995 and last in 2024). There were 19 additional incubating females that were killed in the nestbox during 1992–2024 prior to behavioural sampling and were thus not included here. The average number of breeding attempts recorded each year during 1992–2024 was 26.3 (range 15–40) and, on average, 52.9% (range 13.2–83.3%) of these were depredated per year. The average annual number of breeding attempts that proceeded to incubation was 16.4 (range 7–29). All in all, the 36 killed females constituted, on average, 4.5% (range 0–20.0%) of all breeding attempts and 8.0% (0–33.3%) of breeding attempts that proceeded to incubation. It should be emphasized that while the predation data analysed here are from a population breeding in nestboxes provided by humans, goldeneye face high nest predation by pine marten also in natural cavities. Old nest holes of black woodpecker are frequently used by goldeneyes for nesting (Johnsson et al. 1993), and pine marten is the most important predator of both eggs and incubating females in them, too (Nilsson et al. 1991; Johnsson 1993).

The clutch size was recorded for all nests, including the depredated ones. The timing of the start of egg-laying was back-calculated from the day when a nest with eggs was found, assuming that laying interval between eggs is 1.32 days (Fredga and Dow 1983; Pöysä 2025). It was scaled to annual mean (nest-specific value minus mean of all nests in a given year; hereafter, "relative timing of egg-laying") to take into account among-year variation in the overall timing of nesting when pooling data from different years. Furthermore, we calculated the difference (in days) between the timing of recording female behaviour (if there was more than one behavioural record per female/nest within a season, the mean date was used) and the timing of the start of egg-laying (unscaled original dates used for the start of egg-laying) for each depredated nest (hereafter, "relative timing of recording female behaviour"). This variable indicates the amount of investment (in terms of time) by the female in the nesting attempt, a factor that could potentially affect female behaviour (e.g. Mallory et al. 1998). Considering that incubation takes about 30 days (Eadie et al. 1995), investment of time in egg-laying and incubation of a successful clutch of 8 eggs, for example, is about 41 days. Finally, we calculated the overall nestbox-specific predation risk, i.e. the proportion (percentage) of depredated nesting attempts from all nesting attempts in a nestbox during 1992–2024, for nestboxes with at least five nesting attempts in 1992–2024. This variable was included to check for the possibility that an incubating female was killed just because she used a nestbox with high predation risk. Due to missing values for some variables, the sample size varies among analyses and is therefore presented per analyses.

In addition to the females that faced nest depredation, behavioural data were obtained for females/nesting attempts that proceeded to incubation and were not depredated. Behavioural data from these females were scored in the same way as those from depredated nests and included for annual repeatability analysis (i.e., repeatability analyses were based on data pooled from successful and depredated nests).

Statistical analyses

To prevent clutch desertion due to disturbance, goldeneye females are not captured before the end of incubation. Therefore, the identity of females of nests that were depredated earlier during incubation (or during egg-laying) was not known, except if the carcass was found (see above). This means, for example, that we cannot be sure if two nests depredated in different years, but the female survived, belonged to the same female or two different females. Exceptions are cases in which the female was killed by the predator as all such nests of course belonged to different females. Similarly, because goldeneye females do not lay replacement clutches if the nesting attempt is depredated during incubation, nesting attempts that proceed to incubation represent independent observations (belong to different females) within a season. Because of the complex dependencies in the data, we used a resampling-based bootstrap test (Manly 1991; Crowley 1992; Davison and Hinkley 1997), instead of standard statistical tests, for hypothesis-testing. While inferences from resampling-based bootstrap analyses are specific to the data at hand, they can be done without assumptions of standard statistical tests and models (Manly 1991; Davison and Hinkley 1997). We tested whether females killed during a nest predation event were bolder than females on average among all the females (killed or survived) that faced an equally dangerous predator. To that end, we applied a directional testing approach and calculated the probability of randomly drawing bold females like those in the "killed females" group from the pooled data of killed and survived females. In the cases when more than one behaviour observation per female/nest was recorded within a season, the mean boldness score was used. Hence, 1000 samples of 17 females (i.e. the sample size of killed females' data) were randomly drawn with replacement from the pooled data (killed females' data plus survived females' data $=91$ females in total) and the mean boldness score was calculated for each sample. Then we checked how many of the 1000 bootstrapped mean boldness scores were as large or larger than the observed mean boldness score of the "killed females" group; the number of such cases divided by 1000 gave the probability value for the test. We calculated the 95% confidence intervals for the 1000 bootstrapped means using the basic bootstrap method (Davison and Hinkley 1997). We checked whether the observed mean boldness score of the "killed females" group was within or outside the bootstrapped 95% confidence intervals. The same analysis approach was applied to the other variables, using the sample sizes of the killed females as appropriate, i.e. $n=17$ for relative timing of egg-laying, $n=13$ for clutch size, $n=17$ for relative timing of recording female behaviour and $n=16$ for nestbox-specific nest predation risk.

Repeatability of the boldness behaviour in incubating females was measured using the output of one-way analyses of variance according to the procedure recommended by Lessells and Boag (1987). To ensure independence of observations, repeatability was calculated separately for each year for which behavioural data were available for at least five females with two or more behavioural recordings per female. So, we are here referring to the repeatability of an individual's behaviour during a given breeding season (i.e., over the course of incubation). To study whether there was any consistent change in the boldness behaviour of individual females as incubation proceeded, we calculated Spearman rank correlations between female-specific changes in boldness score between the first and last behavioural observation (boldness score in the last observation minus boldness score in the first observation) and female-specific number of days between the first and last behavioural observation. A positive correlation would indicate that, on average, boldness increases with incubation stage, whereas a negative correlation would indicate the opposite. All nesting attempts that proceeded to incubation (depredated or not) were used to calculate the annual repeatability values and the Spearman rank correlations.

All statistical analyses were performed in SYSTAT 13.

Results

Annual values of repeatability of the boldness behaviour in incubating females ranged from 0.399 to 1.0, with a mean of 0.760 (Table 1; see Fig. S1 for examples). There was no overall tendency for the boldness of individual females to increase (or decrease) towards the end of incubation (Fig. 1), annual rank correlations between change in boldness score (boldness in the last visit by the observer to the nest (last observation) minus boldness score in the first visit by the observer to the nest (first observation)) and time (days) that elapsed between the first and last observations ranging from -0.67 to 0.60 ($p>0.100$ in all cases) with a mean of 0.09 (Table 1). In most cases (87 out of 127), the boldness score did not differ between the first and the last observation (i.e. difference $=0$) regardless of the time difference between the observations (see Fig. 1).

Females that were killed by a predator had higher mean boldness score than females that survived (Fig. 2; Table 2). The bootstrap analysis revealed that the probability of drawing a mean boldness score of 4.5 (mean for the "killed females" group) or larger from the pooled data of killed and survived females was only 0.002 and that the observed mean boldness score of the killed females fell outside the upper 95% confidence interval of the bootstrapped mean (Table 2). Similar bootstrap analyses suggested that the means of the relative timing of egg-laying, clutch size, nest predation risk and relative timing of recording female behaviour of the killed females were not large (or small) compared with the corresponding means in the randomly drawn samples from the pooled data, all the observed means falling within the

Table 1 Repeatability of boldness in incubating goldeneye females and Spearman rank correlation between female-specific changes in boldness score between the first and last behavioural recording (i.e. boldness score in the last recording minus boldness score in the first recording) and female-specific number of days between the first and last recording. Spearman rank correlation could not be calculated for 2013, because none of the nine females showed a change in the boldness score between the first and last recording; the boldness score was consistently 1 for two females and 5 for seven females. All females independent of nest fate (i.e. depredated or not) were included in the data used to calculate repeatability and rank correlations. See Materials and methods for further information

Year	Number of females	Total number of recordings	Range of recordings per female	Repeatability	Spearman rank correlation
2008	5	11	2–3	0.810	0.11
2009	6	20	2–5	0.962	−0.21
2010	11	30	2–5	0.416	0.35
2012	7	23	2–6	0.936	0.14
2013	9	31	2–5	1.000	NA
2014	16	47	2–4	0.821	0.18
2015	7	22	2–5	0.821	−0.36
2016	8	24	2–6	0.805	−0.17
2017	7	15	2–3	0.590	0.27
2018	7	18	2–5	0.827	0.06
2019	10	47	2–7	0.828	0.18
2020	10	38	2–9	0.524	0.15
2021	5	16	2–4	0.861	0.34
2022	5	17	2–5	0.986	0.35
2023	5	13	2–4	0.399	−0.67
2024	9	26	2–5	0.572	0.60

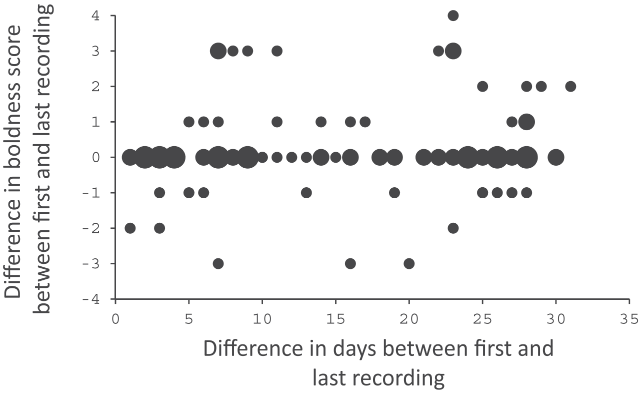

Fig. 1 Overall pattern of change in boldness of individual incubating goldeneye females between the last and first observations in relation to difference in days between the first and last observations. Change in boldness was measured as boldness score in the last observer visit to the nest (last observation) minus boldness score in the first observer visit to the nest (first observation). Data depicted in the Fig. are pooled over years ($n=127$ females/nests); correlations based on annual data are presented in Table 1. Filled circles of different size indicate the number of overlapping data points: small circle = 1 data point; medium circle = 2–4 data points; large circle = >4 data points

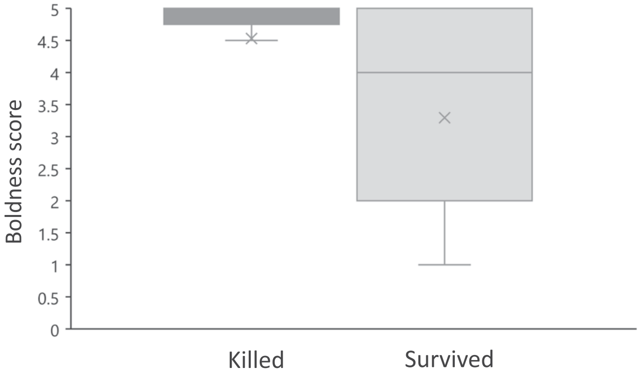

Fig. 2 Box plots of showing mean boldness score of incubating goldeneye females that were killed ($n=17$) during a predator attack and females that survived ($n=74$) a predator attack. Boxes show upper and lower quartiles (x denotes the mean) of the data and whiskers indicate variability (range) outside the quartiles. Possible boldness score values ranged from 1 (shy) to 5 (bold)

95% confidence intervals of the corresponding bootstrapped means (Table 2).

Discussion

Direct links between personality traits and mortality risk has rarely been documented in the wild (see Introduction). As far as we know, the results of this study provide the first evidence that bold incubating avian females risk their lives when a predator attacks. We demonstrated that among all the females that faced a predator that was able to kill females, those females that behaved bold against human-induced disturbance (i.e., boldness was measured independently of the predator attack) along the shy-bold continuum were killed with a high probability. Results of this study further revealed that the goldeneye females that got killed did not have extreme values in terms of nesting characteristics reflecting female experience and condition or in terms of overall predation risk of the nest sites they occupied compared with females in randomly drawn samples from the pooled data of killed and survived females. Hence, boldness was directly associated with higher mortality. Our results thus provide support for the rarely confirmed prediction that

Table 2 Statistics for boldness score, clutch size, relative timing of egg-laying, relative timing of recording female behaviour, and nestbox-specific nest predation risk for incubating goldeneye females that were killed or not during a predator attack. Means (95% confidence intervals) of 1000 bootstrap samples are also given, together with number of the bootstrapped means that were as large or larger (for all but clutch size) or as small or smaller (clutch size) than the corresponding observed mean for killed females. Bootstrapped means were calculated by randomly drawing with replacement 1000 samples from the data pooled from killed and surviving females; sample size was the same as the number of females in the data from "killed females" for a given variable. See Materials and methods for further information

	Killed			Survived			Bootstrap analysis			
	Mean	Range	*N*	Mean	Range	*N*	Mean	Lower 95%	Upper 95%	Larger or smaller (/1000)
Boldness	4.5	2–5	17	3.3	1–5	74	3.5	2.4	4.0	2
Clutch size	8.5	4–15	13	8.9	6–21	65	8.8	6.9	10.0	369
Relative timing of egg-laying	3.6	−16.0–19.5	17	1.3	−18.1–22.0	73	1.6	−4.5	5.5	215
Relative timing of recording female behaviour	19.5	8–41	17	16.9	8–37	73	17.4	13.4	20.0	115
Nestbox-specific predation risk	63.1	7.7–100	16	57.5	22.2–100	58	58.6	44.6	65.6	183

individuals expressing more risky behaviours suffer higher mortality, this being the key prediction of theories explaining the maintenance of behavioural variation among individuals in wild populations (Stamps 2007; Biro and Stamps 2008; Réale et al. 2007; Moiron et al. 2020). Finally, repeatability of female behaviour along the shy-bold continuum appeared to be relatively high, with little variation within individual females but consistent differences among females.

While direct evidence of the link between risk-taking and mortality has not been documented in incubating birds until now, risk-taking behaviour of incubating females and factors potentially affecting it have been studied in many species (e.g. Forbes et al. 1994; Dassow et al. 2012; Graham and Shutler 2019; Redmond et al. 2020; Mohring et al. 2022; Krenhardt et al. 2024). For example, Mohring et al. (2022) studied variation of risk-taking behaviour, measured with flight-initiation distance (FID) during an observer approach, in ground-nesting incubating common eider females (*Somateria mollissima*), another sea duck species, in relation to predation risk of the breeding environment. They found that increased risk-taking (shorter FID) by females was associated with increasing female age and better body condition. Considering that risk-taking by nest defending parents in long-lived species should increase with age (Montgomerie and Weatherhead 1988; but see Graham and Shutler 2019), it is possible that the goldeneye females that got killed were older and, therefore, took more risk. Indeed, Vakili et al. (2025) found that boldness of incubating goldeneye females increased with age, although repeatability of boldness was relatively high across years. On the other hand, females with good body condition and large clutches, both characteristics associated with advancing female age in goldeneyes, common eiders and many other species (Blums et al. 1997; Hanssen et al. 2003; Clark et al. 2014), could be associated with more risk-taking. However, the results concerning relative timing of breeding and clutch size (both being breeding characteristics indicating female age and experience as well as condition) of the killed goldeneye females did not support this hypothesis. We acknowledge that associations between risk-taking behaviour and these female traits in incubating goldeneye females need further investigation with more direct measures of female condition and age. In addition, as found in another goldeneye population, conspecific brood parasitism as an alternative reproductive tactic in goldeneyes (e.g. Pöysä 1999, 2024; Eadie and Savard (2015) may cause complex associations between female traits and boldness behaviour in incubating females (see Vakili et al. 2025). Notwithstanding the preceding, results of this study demonstrate that boldness has a direct fitness cost (mortality risk), fulfilling the fundamental assumption that risky behaviour may mediate trade-offs between current and future reproduction (Moiron et al. 2020). This finding, along with our other study of incubating goldeneye females, which showed that bolder individuals had larger clutches below the parasitism threshold (Vakili et al. 2025), supports the idea that reproductive trade-offs are linked to personality types (Wolf et al. 2007).

The annual repeatability values varied quite a lot: from 0.399 to 1.0. Still, the mean repeatability of the boldness in this study (0.760) was higher than the mean repeatability value (0.37) reported by Bell et al. (2009) from a meta-analysis of published studies across several types of behaviour and several animal taxa. This is probably because we measured repeatability over a relatively short time interval within a breeding season. In line with this suggestion, Bell et al. (2009) found repeatability estimates to be higher for behaviours measured close together in time. Nevertheless, our study provides additional support for consistent individual differences in behaviour in wild populations. Vakili et al. (2025) in turn demonstrated that boldness of incubating goldeneye females is repeatable across years. Related to repeatability, boldness of individual females did not consistently change with advancing incubation, although there was some variation among females in this pattern. This finding differs somewhat from that of Mallory et al. (1998), who reported that, when they used data from first visits to the nest only, female goldeneyes allowed observers to approach closer to the nest before flushing as incubation proceeded, an observation consistent with the prediction that females should invest more in nest defence as incubation proceeds (Montgomerie and Weatherhead 1988; Mallory et al. 1998). Interestingly, Mallory et al. (1998) also found that incubating goldeneye females that had been visited at least once earlier in incubation during the same season modified their response and flushed while the observer was farther away on subsequent visits. Based on these results, the authors concluded that goldeneye females do not habituate to visitors. While we did not find a corresponding increase in flushing distance (decrease in boldness), our results are generally in line with the conclusion of Mallory et al. (1998) in that we did not observe consistent changes in boldness of individual females during the incubation period. On the other hand, the observed variation among females in how the risk-taking behaviour changed as incubation proceeded suggests that there may have been among-female variation in short-term dynamics of some intrinsic state variable. For example, foraging success during incubation recesses may have affected daily mass changes and short-term energy deficits, affecting female incubation (Mallory and Weatherhead 1993). Our study design did not allow to consider short-term variation in female-specific energy deficits, because we did not know when a given female had been off the nestbox for foraging before the behaviour was recorded. As has been found for risk-taking in foraging contexts, fluctuating energy reserves may importantly affect individual behaviour (e.g. Wolf and Weissing 2010; Sih et al. 2015; Moran et al. 2021). While not affecting the main finding of this study (overall association between boldness and mortality), possible short-term within-individual variation in energy reserves may have resulted in an underestimation of the repeatability. All in all, the role of short-term fluctuation in energy reserves in affecting risk-taking behaviour of incubating females is a topic that deserves further research.

The findings of this study have important population level implications. In general, adult female mortality and reproductive output are demographic traits with potentially strong influences on population growth rate (Anderson et al. 1997; Flint 2015; Koons et al. 2017). Killing of incubating females, in particular, has fundamental population level consequences for two reasons. In addition to losing their reproductive output in the year in question, prime reproductive-age females are lost from the population. Indeed, Lawson et al. (2017) found in goldeneyes that adult female survival had a greater proportional influence on population growth than did recruitment. High mortality of incubating females may result in biased adult sex ratios, which in turn may negatively affect reproductive output and viability of populations (Donald 2007; Székely et al. 2014). In this study area, the annual percentage of killed females of females that attempted to nest and of females the nesting attempt of which proceeded to incubation was relatively high (see Materials and methods). An important avenue for further research would be to find out the role of mortality of bold incubating females in affecting population dynamics in goldeneyes and other species with high mortality of incubating and brood-caring females (e.g. Arnold et al. 2012 and references therein). This research need is particularly urgent in the goldeneye and some other duck species for which data from the national waterfowl monitoring scheme in Finland suggest that both breeding numbers and reproductive output are in a long-term decline (Piha et al. 2024).

In conclusion, our study provides the first direct evidence of higher mortality of bold incubating avian females compared with less bold females. This is an important finding, considering that the previously widely upheld idea that life-history trade-offs explain the maintenance of behavioural variation among individuals in wild populations has recently been questioned, one of the main reasons for this being that support for survival costs of various behavioural traits is limited (Moiron et al. 2020; Haave-Audet et al. 2022). In contrast, our study together with Møller (2013), Santos et al. (2015), Hulthén et al. (2017) and Ward-Fear et al. (2018) provide strong direct evidence of survival cost of risk-taking in free-ranging animals of several taxa, including lizards, fish and birds. Hence, direct evidence of survival costs to boldness in the wild is accumulating, suggesting that predation risk is an important selection pressure in the evolution and maintenance of among-individual variation in behavioural traits in natural populations. It is challenging to gather data with which survival cost of risk-taking behaviour can be studied under natural conditions, but more such studies are needed to enhance understanding of conditions under which risky behavioural types would or would not incur a survival cost.

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Data availability All data supporting the findings of this study are available within the paper and its Supplementary Information.

Declarations

Ethical approval Field work was done in accordance with Finnish and EU Laws and regulations and under the bird ringing licence (no. 717 to HP) by Ringing Centre of the Finnish Museum of the Natural History. Ethical approval from ethics committee for involving animals in this study was not required.

Conflict of interest None.

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