Flushing distance of incubating Common Pochard *Aythya ferina* females from nests: effects of clutch value and environmental conditions

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Abstract

Birds have evolved diverse behaviours to defend their nests and themselves against predators, ranging from active defence to flushing at a distance. Previous waterfowl studies showed biotic and abiotic factors influence females' flushing behaviour from nests when disturbed by predators. Here, factors potentially affecting flushing distances of incubating Common Pochard *Aythya ferina* females were examined in a wetland with variable water levels. Females were predicted to exhibit riskier behaviour with increasing clutch value, flushing at shorter distances (*i.e.* assuming a higher risk) from nests with larger clutch sizes, earlier in the nesting season than later, and during hatching rather than incubation or laying. Support for the clutch value hypothesis was mixed: females with larger clutches generally flushed from their nests at shorter distances; they also flushed at shorter distances during hatching than incubation, and likewise during incubation than laying. However, laying date did not affect the flushing distance. Females flushed at greater distances in deeper water levels, suggesting enhanced predator detection or reduced vulnerability in deeper water, but the presence of colonial nesting waterbirds did not affect flushing distances for Pochard in this study. These results indicate that Pochard nest-defence decisions reflect trade-offs between the clutch value and female survival, shaped by biological and environmental factors.

Key words: clutch-size, individual vulnerability, nest defence, nesting conditions, parental behaviour, risk-taking.

Predation is a primary cause of nest loss in birds (Ricklefs 1969), especially among ground-nesting species, and birds have evolved behaviours to defend their nests against predators (Caro 2005). Numerous studies have examined nest defence strategies based on predictions from parental investment theory (*e.g.* Redondo & Carranza 1989; Amat *et al.* 1996; Sergio & Bogliani 2001), in which parents must balance the prospects for future reproduction with the value of their current brood (Trivers 1972). It has been hypothesised that the intensity of nest defence correlates with offspring

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number (Montgomerie & Weatherhead 1988; Redondo 1989) and/or brood age, likely because older broods have received greater parental investment and have higher survival prospects than younger broods (Andersson *et al.* 1980), prompting parents to invest in stronger nest defence for older broods. Risk to adult survival is another factor that may influence nest defence decisions. Additionally, intrinsic factors, such as the parents' age, body condition and body size, or previous experience with predation attempts, also affect nest defence levels (Knight *et al.* 1987; Dassow *et al.* 2012; de Jong *et al.* 2021; Vakili *et al.* 2025).

In many cases, breeding birds perform distraction displays to deceive predators, but active deception can carry risks for adults (*e.g.* Sanders & Maloney 2002). Departing surreptitiously from the nest might serve as an alternative strategy to avoid nest predation. This more passive behaviour includes birds moving off the nest when a potential predator is some distance away and can be regarded as a form of nest defence (Forbes *et al.* 1994; Smith & Edwards 2018; Sanchez-Gomez *et al.* 2024).

In addition to biological factors, female flushing behaviour from nests during predator disturbance may be affected by abiotic factors. Responses of incubating adults could relate to their own vulnerability to predation or environmental stressors that threaten egg viability (Dale *et al.* 1996). Early predator detection may also be facilitated on nesting close to a colonial-breeding species, for instance by recognising the colonial species' alarm call and responding by immediately leaving their nest (Nuechterlein 1981).

Previous research on waterfowl shows that biotic and abiotic factors influence female flushing behaviour from nests when disturbed by predators. Females tend to flush closer to nests, or to sit tight, later in incubation (Hochbaum 1944; Forbes *et al.* 1994; Mallory *et al.* 1998; Gunness & Weatherhead 2002; Albrecht & Klvaňa 2004; Osiejuk & Kuczyński 2007; Quilfeldt *et al.* 2005; Clermont *et al.* 2019; de Jong *et al.* 2021). In some cases, however, the stage of incubation had no effect (Miller *et al.* 2013). Results regarding clutch sizes were likewise mixed: some studies found that females laying larger clutch sizes flushed at shorter distances (Forbes *et al.* 1994; Albrecht & Klvaňa 2004; Quilfeldt *et al.* 2005; Vakili *et al.* 2025), while others did not (Mallory *et al.* 1998; Gunness *et al.* 2001). In one case, females with smaller clutch sizes even flushed at closer distances than those with larger clutches (Osiejuk & Kuczyński 2007). Environmental factors such as interannual variations in precipitation (Gunness *et al.* 2001) or vegetation cover (Albrecht & Klvaňa 2004; Osiejuk & Kuczyński 2007; Miller *et al.* 2013; Mohring *et al.* 2022) also influenced the flushing distance (hereafter FD). Additionally, the frequency with which researchers visited nests affected FDs in some cases (Mallory *et al.* 1998; Gunness & Weatherhead 2002), but not in others (Osiejuk & Kuczyński 2007; Miller *et al.* 2013). The variability across studies in the responses of incubating female waterfowl to disturbance may be attributable to differences in the natural history of the species or to a lack of statistical control of some variables over others in some analyses.

Here, the flushing behaviour of Common Pochard *Aythya ferina* (hereafter Pochard) females from nests in a wetland experiencing seasonal and annual variations in water levels was analysed. Based on theoretical predictions and previous studies, it was expected that females would flush from disturbance closer to their nests: (1) when their clutch sizes were larger, and (2) during the later stages of incubation. Given that Pochard take flight by running on water before becoming airborne, and because very low water levels could affect take-off, (3) greater FDs in very shallow water would be required, as females would be more vulnerable to predators under such conditions. In addition, (4) the effect of the presence of colonial-nesting waterbirds near Pochards' nests was examined. It was expected that Pochard would flush at longer distances from their nests when nesting near colonial-breeding waterbirds because the alarm calls of the colonial birds would warn of the presence of a predator in the area and, by flushing at longer distances, the Pochard would reduce the risk of being killed. Alternatively, because colonial waterbirds attack predators, the incubating Pochard may perceive a lowered predation risk, and the FDs would not be affected.

Methods

Study site and field procedures

The study was conducted between 1985 and 1989 in the Guadiamar Nature Reserve, within the Doñana National Park (Guadalquivir marshes, southwest Spain, 37º00'N, 6º20'W). Interannual variation in the extent of flooding occurs, decreasing from spring to early-mid summer, when the area usually dries out (Amat 1981). In this area, the Pochard nests from April to June in flooded sites, specifically in old watercourses (locally known as "quebradas") and in channels ("caños") (Amat 1982). The vegetation of these habitats is described in Amat (1982) and Ibáñez *et al.* (2023).

Nests were encountered while riding horseback through the study area. Egg collection of many waterbird species was frequent during the first half of the 20th century in southern Spain (Valverde 1960), making humans an appropriate model predator of duck nests. The Pochard likely became alert when they heard splashing as the horse approached in flooded sites. When a female flushed, the distance from the nest was estimated by pacing (human steps: 1 step = *c.* 0.7 m), the definition adopted here for flushing distance (FD). Water depth at the nesting site was recorded to the nearest cm using a tape. The number of eggs and whether the nest was in the laying, incubation or hatching stage were also recorded. Nests were deemed to be at the laying stage when they contained little down and the eggs were cool. Pochard parasitises both intra- and interspecifically (Amat 1982, 1985; Neužilová & Musil 2010), but all parasitised nests were excluded from this study. A nest was considered to be intra-specifically parasitised when: (1) it contained > 14 eggs, (2) more than one egg was laid during a day, and/or (3) eggs were laid after incubation commenced. Lastly, whether the nests were located inside or within 100 m of a breeding colony of waterbirds (Black-winged Stilts *Himantopus himantopus*, or in a few cases Pied Avocets

Recurvirostra avosetta and Whiskered Terns *Chlidonias hybrida*) was also recorded. This cutoff distance was chosen because it approximates to the distance at which stilts begin to emit alarm calls as an observer approaches. The size of those colonies varied between 10 and slightly more than 100 nests.

The nests were visited between 1–4 times. Laying dates were estimated using two methods: (1) for nests found during the laying stage, the eggs were counted and onset of laying was backdated to the first egg, assuming a 1-day laying interval between eggs, and (2) for nests found at hatching, the incubation period (26 days; Cramp & Simmons 1977) was used to backdate, with egg-laying intervals added according to the clutch size. The laying date was expressed as a laying day relative to 1st March. Not all data were available for each nest. For instance, laying dates could not be determined for all nests found during the incubation stage, because some were deserted or predated, and others hatched before the last visit. Consequently, sample sizes may vary between statistical analyses.

Statistical analyses

To ensure that repeat visits to a nest did not affect FD measures (*e.g.* through habituation), only the first visit to every nest was considered. Statistical analyses were conducted using jamovi software (The jamovi Project 2024). Ideally, model selection assesses the effect of all factors and covariates being considered, using the Akaike Information Criterion (AIC) to compare different models (Burnham & Anderson 2002). In this study, however, sample sizes using all data would have varied significantly among models (*e.g.* if including laying date and nesting stage), so an AIC-based selection approach was not used on considering all nests (n = 205) because differences in sample sizes would bias likelihood estimates and AIC comparisons. If the model has many parameters relative to the sample size, as was the case for some variables, this can lead to overfitting and unreliable estimates. Only nests with the more complete dataset (n = 122), where the main explanatory variables (*i.e.* year, presence of colonial waterbirds, water depth and clutch size) were all recorded, therefore were included in comparison of the models.

Generalised linear models (GLMs) with Poisson distribution and log-link function were used to analyse the flushing behaviour of females, using the distance at which females flushed from nests (number of steps) as the dependent variable, year (1985–1989), and presence of colonial waterbirds (yes if < 100 m; no if > 100 m) as factors, and water depth (cm) and clutch size (excluding parasitised nests) as covariates. The initial model included all main effects and a two-way interaction, whilst the best models were selected using the AIC for small samples (AICc). Models with the lowest AICc were considered the best for explaining variability in FD from nests, with those where the difference in AICc values (ΔAICc) was < 2 having similar support.

Variables for which there were fewer data were analysed using univariate statistics. A Spearman's rank correlation was used to determine the effect of laying date on FDs, whilst distances at which Pochard flushed

from their nests during the different nesting stages were compared using Kruskal-Wallis ANOVA.

Results

The best model explaining the FDs of female Pochards from their nest accounted for 19% of the variance (adjusted $R^2 = 0.191$, $P < 0.001$; Table 1). It included the additive effects of water depth, clutch size, the presence of colonial waterbirds and year, as well as the interaction between the presence of colonial waterbirds and year. A model excluding clutch size as a covariate was also supported, explaining slightly less variance (adjusted $R^2 = 0.187$, $P < 0.001$; Table 1).

In the best model, water depth (range: 0–50 cm) positively affected FDs (Fig. 1), and this effect was highly significant (Table 2). Clutch size (range: 5–14) also affected FDs, with females with larger clutch sizes flushing at significantly shorter distances (Fig. 2, Table 2). The presence of colonial waterbirds did not in itself affect FD (Fig. 3A, Table 2). Females flushed from nests at shorter distances in 1985 than during 1987–1989 (Fig. 3B, Table 2). There was an interaction between year and the presence of waterbird colonies: Pochard flushed at shorter distances when there were waterbird colonies present in 1986, compared with 1985; conversely, females flushed at greater distances when there were waterbird colonies present in 1989 (Fig. 3C, Table 2).

On considering only nests at the incubation stage, there was no relationship between laying date and FD (Spearman's rank correlation: $r_s = 0.195$, $n = 17$, $P = 0.454$). Regarding nesting stages, females flushed at longer distances from nests during laying than during incubation; in addition, they flushed at longer distances during incubation than during hatching

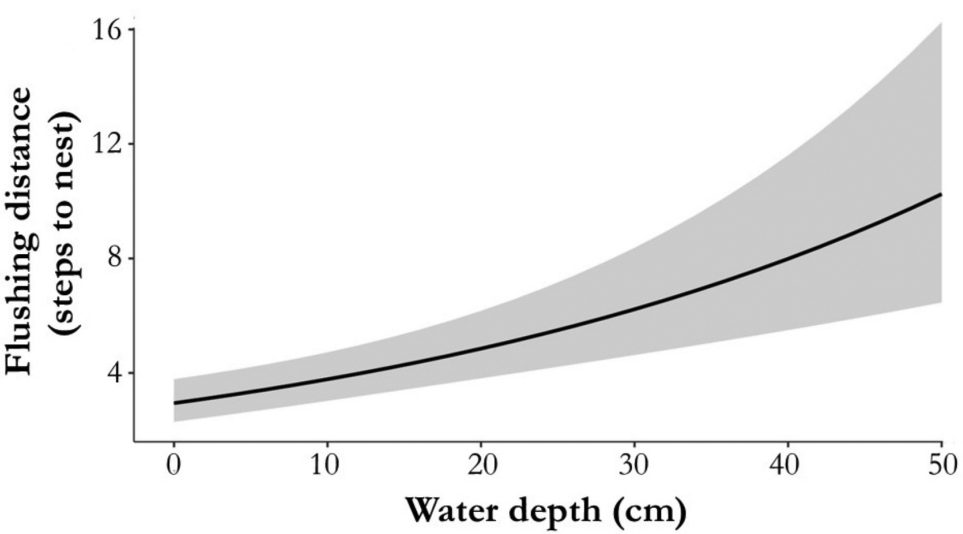


Figure 1. Flushing distance of Pochard females from their nests in relation to water depth at the nesting sites. The regression line and confidence intervals are derived from Model 1 in Table 1.

Table 1. Summary of Generalised Linear Models (GLM) used to determine the effects of water depth (WD), clutch size (CS), presence of waterbird colonies (WC) and year (YR) on flushing distances (FD) of incubating Pochard females from nests. The best supported models, according to ΔAICc, are in bold.

Model	Expression	R^2	Adjusted R^2	AICc	ΔAICc
1	**FD ~ 1 + WD + CS + YR + WC + YR×WC**	**0.208**	**0.191**	**874.999**	**0**
2	**FD ~ 1 + WD + YR + WC + YR×WC**	**0.202**	**0.187**	**876.598**	**1.599**
3	FD ~ 1 + YR + WC + YR×WC	0.176	0.162	891.536	16.537
4	FD ~ 1 + CS + YR + WC + YR×WC	0.178	0.163	892.312	17.313
5	FD ~ 1 + WD + CS + YR + WC	0.156	0.146	899.540	24.541
6	FD ~ 1 + WD + YR + WC	0.151	0.142	901.118	26.119
7	FD ~ 1 + WD + CS + YR	0.149	0.140	902.284	27.285
8	FD ~ 1 + WD + YR	0.142	0.135	904.510	29.511
9	FD ~ 1 + CS + YR + WC	0.132	0.123	913.805	38.806
10	FD ~ 1 + YR	0.106	0.100	926.330	51.331
11	FD ~ 1 + CS + YR	0.108	0.101	926.982	51.983
12	FD ~ 1 + WD + CS + WC	0.051	0.046	961.114	86.115
13	FD ~ 1 + CS + WC	0.044	0.041	963.626	88.627
14	FD ~ 1 + WD + WC	0.038	0.035	967.295	92.296
15	FD ~ 1 + WC	0.035	0.033	967.414	92.415
16	FD ~ 1 + WD + CS	0.033	0.030	970.861	95.862
17	FD ~ 1 + WD	0.016	0.014	980.057	105.058
18	FD ~ 1 + CS	0.011	0.009	983.374	108.375

R^2 values measure the proportion of variance in the dependent variable that the predictors in the model explain, and adjusted R^2 values refer to the proportion of variance explained after adjusting for the number of predictors and sample size. Model predictability was evaluated using the Akaike Information Criterion corrected for small samples (AICc).

(Kruskal-Wallis ANOVA: $\chi^2_2 = 8.22$, $P = 0.016$). In the three cases in which females were approached at hatching, they flew directly from the nest (Fig. 4).

Discussion

The results of this study indicate that FDs of female Pochards in response to

Table 2. Influence of variables included in the best model (see Table 1) explaining the flushing behaviour of incubating Pochard females from their nests. YR = year, WC = presence of waterbird colonies, WD = water depth and CS = clutch size. Parameter estimates (with standard errors, s.e.), exponential of regression coefficients Exp(β), and their lower and upper confidence intervals (CI) are shown.

			Exp(β) 95% CI				
Variable	**Effect**	**Estimate (s.e.)**	**Exp(β)**	**Lower**	**Upper**	**z**	***P***
(Intercept)	(Intercept)	1.371 (0.113)	3.938	3.154	4.916	12.106	< 0.001
YR1	1986–1985	–0.071 (0.522)	0.931	0.335	2.591	–0.136	0.891
YR2	1987–1985	0.414 (0.186)	1.513	1.050	2.179	2.224	0.026
YR3	1988–1985	0.478 (0.138)	1.612	1.231	2.112	3.468	0.001
YR4	1989–1985	0.980 (0.215)	2.665	1.749	4.063	4.558	< 0.001
WC1	Yes/No	–0.038 (0.227)	0.963	0.617	1.504	–0.166	0.868
WD	WD	0.023 (0.005)	1.024	1.014	1.034	4.628	< 0.001
CS	CS	–0.038 (0.019)	0.963	0.928	0.999	–2.001	0.045
YR1 × WC1	(1986–1985) × (Yes/No)	2.399 (1.042)	11.014	1.428	84.943	2.302	0.021
YR2 × WC1	(1987–1985) × (Yes/No)	0.150 (0.361)	1.161	0.572	2.357	0.415	0.678
YR3 × WC1	(1988–1985) × (Yes/No)	0.509 (0.278)	1.663	0.965	2.866	1.832	0.067
YR4 × WC1	(1989–1985) × (Yes/No)	–0.982 (0.421)	0.375	0.164	0.854	–2.335	0.020

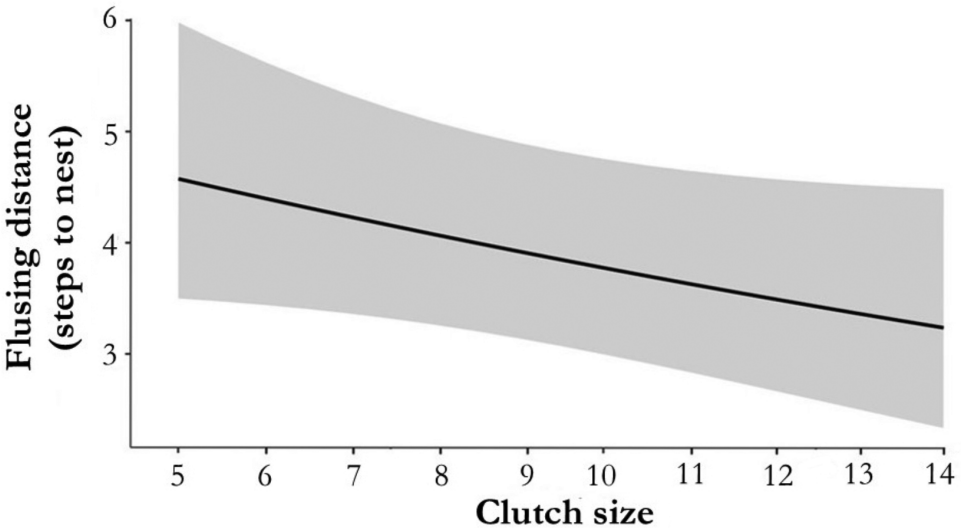


Figure 2. Flushing distance of Pochard females from their nests in relation to clutch size. The regression line and confidence intervals are derived from Model 1 in Table 1.

disturbance during incubation were positively associated with water depth and negatively associated with clutch size. FDs also varied among years and were influenced by an interaction between year and the presence of colonial waterbirds. In addition, the nesting stage affected FDs, whereas neither laying date nor the presence of colonial waterbirds alone showed a significant effect.

Overall, support for the clutch value hypothesis was mixed. Females took greater risks (*i.e.* flushed at shorter distances) when clutch sizes were larger and when embryos were at more advanced developmental stages, but laying date did not influence FD (as reported for dabbling ducks, Forbes *et al.* 1994).

Contrary to predictions (see above), females flushed at greater distances in deeper water, perhaps because movement through deeper water generates more noise. Breeding birds increase vigilance under noisy conditions (Matyjasiak *et al.* 2026) so approach in deeper water may heighten alertness in breeding Pochard, resulting in earlier potential predator responses. This may suggest females assess their own vulnerability when deciding whether to leave the nest. Shallower water sites may support greater vegetation cover, reducing visibility of Pochard females from the nest. Most Pochard nested in old water courses (Amat 1982) with homogeneous cover of Glaucous Glasswort *Arthrocnemum macrostachyum* and Somerset Rush *Juncus subulatus*. Alternatively, females may be able to move faster in deeper water to escape more rapidly from the nest.

There were interannual variations in FDs. Gunness *et al.* (2001) reported that female dabbling ducks flushed at greater distances from their nests in wetter years, and

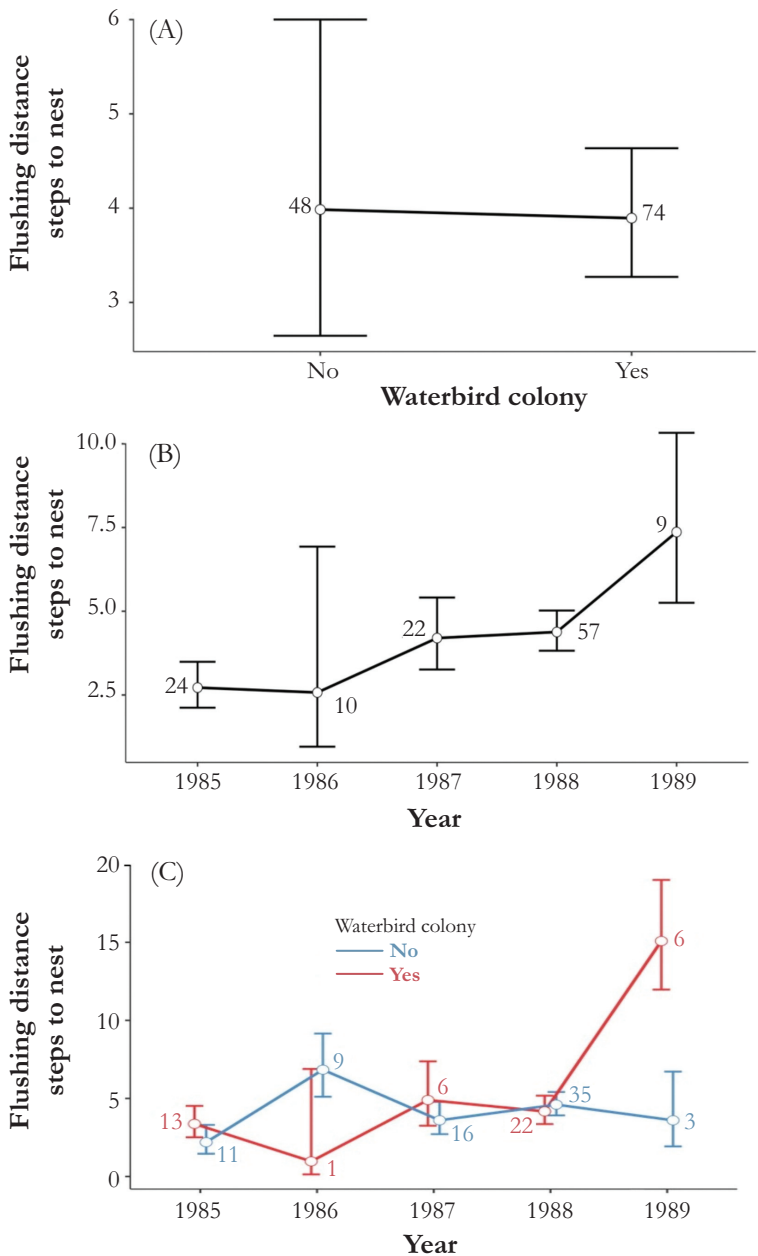


Figure 3. Predicted patterns of variation (means ± s.e. and sample sizes) showing flushing distances of Pochard females from nests according to: (A) whether waterbird colonies were nearby, (B) year and (C) whether waterbird colonies were nearby for each year. Mean and s.e. values are derived from Model 1 in Table 1.

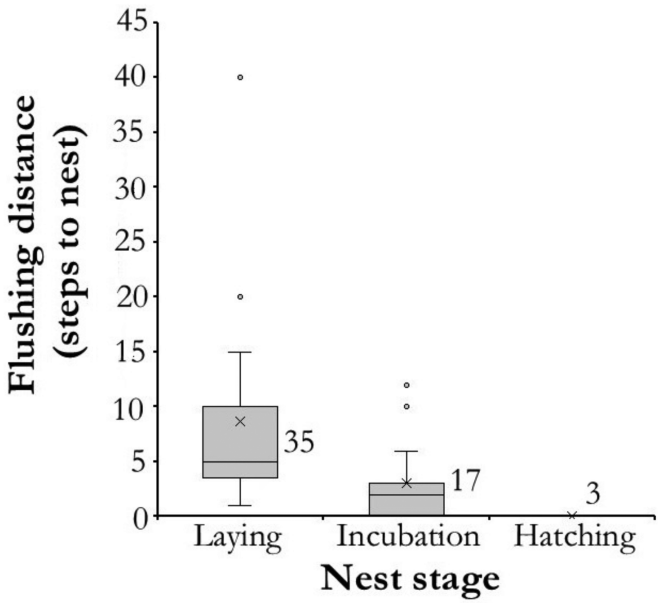


Figure 4. Box-plots for the distances at which Pochard females flushed from nests according to nesting stage. The boxes represent the interquartile ranges (IQR: 25th and 75th percentiles), lines within the boxes represent the medians, and × symbols represent the means. Whiskers extend 1.5 × IQR from the 75th and 25th percentiles. Sample sizes are beside the boxes; dots denote outliers.

suggested that reduced parental investment may enhance the potential for future reproduction through increased post-breeding survival. Under this hypothesis, the greatest FDs in the present study would be expected in 1985 and 1988, the years with the highest rainfall; however, this pattern was not observed (Fig. 3C). It is possible that one or more unmeasured variables influenced the observed interannual variation in FDs. Such variables may also have affected the interaction between year and the presence of colonial waterbirds on FDs.

The hatching success of Pochard in the Guadalquivir marshes increased when nests were located inside breeding colonies of waterbirds (Amat 1982). However, the present study found no relationship between FD and the presence of such colonies. Nest defence theory predicts that incubating birds will flush from the nest when the risk of remaining at the nest exceeds a threshold at which the costs of staying outweigh those of leaving (Montgomerie & Weatherhead 1988; Redondo 1989). For Pochard, once a predator has been detected, the trade-off between the costs and benefits of remaining at the nest may be similar regardless of the proximity of colonial waterbirds when the threat comes from a terrestrial predator (*i.e.* a mammal). This may be the case because Black-winged Stilts may not be very effective at deterring mammalian predators from entering their breeding sites, in which

case flight initiation distances may not differ between sites with and without nearby colonial birds. In contrast, for aerial predators, females nesting near colonial waterbirds may benefit from remaining at the nest after detecting a predator, under the expectation that the collective mobbing behaviour of colonial waterbirds could deter the predator from staying in the area.

Although the GLM result was highly significant, the best model explained only 19% of the variance in FD. While the nesting stage also influenced FD, it could not be included in the final model due to a lack of convergence. Other potential factors affecting FD, both intrinsic (*e.g.* female age, body condition) and extrinsic (*e.g.* nest camouflage, ambient temperature), were not analysed here but previous studies have found that females in better body condition allow closer approaches (Seltmann *et al.* 2012; Mohring *et al.* 2022) and body size differences between species were found to affect FD in one case (Dassow *et al.* 2012). The sightlines of incubating adults on the nest may facilitate early predator detection, enabling the bird to depart at a greater distance from the predator (Amat & Masero 2004). Nest crypsis also influences FD, as birds tend to allow closer approaches by predators when their nests are better camouflaged (Albrecht & Klvaňa 2004; Amat *et al.* 2017; Mohring *et al.* 2022). Lastly, ambient temperature may influence FDs, which tend to be shorter when the risk of unattended eggs overheating due to direct solar radiation is higher (Pereira & Amat 2010; Amat *et al.* 2017), or when the risk of egg cooling also is higher (Graham & Shutler 2019). Female presence on the nest is crucial for maintaining consistent egg incubation temperature, and thus hatching success, under both of these conditions (*e.g.* Miller & Delehanty 2024).

Effects of duck nest parasitism on FDs have been considered in only two studies: one found no effect (Mallory *et al.* 1998), the other showed parasitised females tolerated closer approaches (Vakili *et al.* 2025). Pochard females exhibit limited defensive behaviour against brood parasites (Honza *et al.* 2009). Although parasitised females in the Guadalquivir marshes tended to tolerate closer approaches, the relationship between nest parasitism (intraspecific, interspecific, or both) and FDs was not significant after controlling for clutch size (J.A. Amat, unpubl. data).

Nesting waterfowl are known to defecate on their eggs when disturbed as a defensive mechanism, with the strong faecal odour likely acting as a deterrent (Townsend 1966; Swennen 1968; McDougall & Milne 1978). This behaviour occurs regularly in some species (*e.g.* the Common Eider *Somateria mollissima*), less frequently in others, perhaps as a last-resort strategy once a predator has located the nest. Indeed, Eiders typically flush at close approach by intruders, whereas females of other species often defecate on eggs when surprised on the nest. In this study, Pochards defecated on eggs in only four out of 247 cases (including nests with multiple visits), in three of which females flew directly from the nest, whereas females failed to defecate on eggs in 52 of 247 cases when they flushed directly from the nest. Hence, defecation on eggs does not appear to be an important nest defence mechanism for Pochard.

Conclusions

Overall, these results suggest that flushing behaviour in female Pochard is shaped by clutch value and female vulnerability related to environmental conditions. Consistent with the clutch value hypothesis, females accepted greater risk by flushing at shorter distances when the clutch size was larger and as offspring development advanced. At the same time, the strong positive effect of water depth on FD supports the importance of female vulnerability: in deeper sites, where approaching predators may be detected earlier, females responded more cautiously, likely departing sooner from nests and flushing at greater distances. Taken together, these findings indicate that in nest defence decisions the Pochard females respond to a dynamic balance between the reproductive value of the clutch and their own survival prospects, rather than being driven by a single factor.

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References

Albrecht, P. & Klvaňa, P. 2004. Nest crypsis, reproductive value of a clutch and escape decisions in incubating female Mallards *Anas platyrhynchos*. *Ethology* 110: 603–613.

Amat, J.A. 1981. Descripción de la comunidad de patos del Parque Nacional de Doñana. *Doñana Acta Vertebrata* 8: 125–158.

Amat, J.A. 1982. The nesting biology of ducks in the Marismas of the Guadalquivir, southwestern Spain. *Wildfowl* 33: 94–104.

Amat, J.A. 1985. Nest parasitism of Pochard *Aythya ferina* by Red-crested Pochard *Netta rufina*. *Ibis* 127: 255–262.

Amat, J.A. & Masero, J.A. 2004. Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour* 67: 293–300.

Amat, J.A., Carrascal, L.M. & Moreno, J. 1996. Nest defence by Chinstrap Penguins *Pygoscelis antarctica* in relation to offspring value and age. *Journal of Avian Biology* 27: 177–179.

Amat, J.A., Gómez, J., Liñán-Cembrano, G., Rendón, M.A. & Ramo, C. 2017. Incubating terns modify risk-taking according to diurnal variations in egg camouflage and ambient temperature. *Behavioral Ecology and Sociobiology* 71: 72.

Andersson, M., Wiklund, C.G. & Rundgren, H. 1980. Parental defence of offspring: a model and an example. *Animal Behaviour* 28: 536–542.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference. Second Edition*. Springer, New York, USA.

Caro, T. 2005. *Antipredator Defenses in Birds and Mammals*. University of Chicago Press, Chicago, USA.

Clermont, J., Réale, D., Lindsay, M.È. & Giroux, J.-F. 2019. Plasticity, state-dependency, and individual consistency in Canada Goose nest defense behavior. *Behavioral Ecology and Sociobiology* 73: 66.

Cramp, S. & Simmons, K.E.L. 1977. *The Birds of the Western Palearctic. Vol. I*. Oxford University Press, Oxford, UK.

Dale, S., Gustavsen, R. & Slagsvold, T. 1996. Risk taking during parental care: a test of three hypotheses applied to the Pied Flycatcher. *Behavioral Ecology and Sociobiology* 39: 31–42.

Dassow, J.A., Eichholz, M.W., Stafford, J.D. & Weatherhead, P.J. 2012. Increased nest defence of upland-nesting ducks in response to experimentally reduced risk of nest predation. *Journal of Avian Biology* 43: 61–67.

de Jong, M.E., Nicolaus, M., Fokkema, R.W. & Loonen, M.J.J.E. 2021. State dependence explains individual variation in nest defence behaviour in a long-lived bird. *Journal of Animal Ecology* 90: 809–819.

Forbes, M.R.L., Clark, R.G., Weatherhead, P.J. & Armstrong, T. 1994. Risk-taking by female ducks: intra- and interspecific tests of nest defense theory. *Behavioral Ecology and Sociobiology* 34: 79–85.

Graham, K.F. & Shutler, D. 2019. How robust are risk-taking associations in incubating birds? A test and a review. *Behavioral Ecology and Sociobiology* 73: 79.

Gunness, M.A. & Weatherhead, P.J. 2002. Variations in nest defense in ducks: methodological and biological insights. *Journal of Avian Biology* 33: 191–198.

Gunness, M.A., Clark, R.G. & Weatherhead, P.J. 2001. Counterintuitive parental investment by female dabbling ducks in response to variable habitat quality. *Ecology* 82: 1151–1158.

Hochbaum, H.A. 1944. *The Canvasback on a Prairie Marsh*. University of Nebraska Press, Lincoln, USA.

Honza, M., Piálková, R., Albrecht, T. & Neužilová, Š. 2009. Nest defence against conspecific intruders in the Common Pochard *Aythya ferina*: natural observations and an experimental test. *Acta Ornithologica* 44: 151–158.

Ibáñez, F., Calderón, J. & Amat, J.A. 2023. Breeding biology of the Northern Pintail *Anas acuta* at the edge of its southwestern Palearctic range. *Wildfowl* 73: 134–145.

Knight, R.L., Grout, O.J. & Temple, S.A. 1987. Nest defense of the American Crow in urban and rural areas. *Condor* 89: 175–177.

Mallory, M.L., McNicol, D.K. & Walton, R.A. 1998. Risk-taking by incubating Common Goldemeyes and Hooded Mergansers. *Condor* 100: 694–701.

Matyjasiak, P., Książka, P. & Chacińska, P. 2026. Beyond noise playback: the effect of an audible and visible sound source on bird flushing behavior. *Journal of Ethology* 44: 49–58.

McDougall, P. & Milne, H. 1978. The anti-predator function of defecation on their own eggs by female Eiders. *Wildfowl* 29: 55–60.

Miller, P.C. & Delehanty, D.J. 2024. Thermal ecology of Trumpeter Swan *Cygnus buccinator* incubation. *Wildfowl* (Special Issue No. 7): 131–158.

Miller, V., Abraham, K.F. & Nol, E. 2013. Factors affecting the responses of female Canada Geese to disturbance during incubation. *Journal of Field Ornithology* 84: 171–180.

Mohring, B., Angelier, F., Jaatinen, K., Steele, B., Lönnberg, E. & Öst, M. 2022. Drivers of within- and among-individual variation in risk-taking behaviour during reproduction in a long-lived bird. *Proceedings of the Royal Society B* 289: 20221338.

Montgomerie, R.D. & Weatherhead, P.J. 1988. Risks and rewards of nest defence by parent birds. *Quarterly Review of Biology* 63: 167–187.

Neužilová, Š. & Musil, P. 2010. Inter-specific egg recognition among two diving ducks species, Common Pochard *Aythya ferina* and Tufted Duck *Aythya fuligula*. *Acta Ornithologica* 45: 59–65.

Nuechterlein, G. 1981. 'Information parasitism' in mixed colonies of Western Grebes and Forster's Terns. *Animal Behaviour* 29: 985–989.

Osiejuk, T.S. & Kuczyński, L. 2007. Factors affecting flushing distance in incubating female Greylag Geese *Anser anser*. *Wildlife Biology* 13: 11–18.

Pereira, A.I. & Amat, J.A. 2010. Nesting of the Double-striped Thick-knee (*Burhinus bistriatus*) in a hot environment. *Ornitología Neotropical* 21: 149–154.

Quilfeldt, P., Strange, I.J. & Masello, J.F. 2005. Escape decisions of incubating females and sex ratio of juveniles in the Upland Goose *Chloephaga picta*. *Ardea* 93: 171–178.

Redondo, T. 1989. Avian nest defence: theoretical models and evidence. *Behaviour* 110: 161–195.

Redondo, T. & Carranza, J. 1989. Offspring reproductive value and nest defense in the Magpie (*Pica pica*). *Behavioural Ecology and Sociobiology* 25: 369–378.

Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9: 1–48.

Sanchez-Gomez, S., Lees, D., Weston. M.A. & Maguire, G.S. 2024. When passive nest defence is active: support of the leave early and avoid detection hypothesis in a plover. *Ibis* 166: 1329–1337.

Sanders, M.D. & Maloney, R.F. 2002. Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: A 5-year video study. *Biological Conservation* 106: 225–236.

Seltmann, M.W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K. & Hollmén, T. 2012. Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female Eiders. *Animal Behaviour* 84: 889–896.

Sergio, F. & Bogliani, G. 2001. Nest defense as parental care in the Northern Hobby (*Falco subbuteo*). *Auk* 118: 1047–1052.

Smith, P.A. & Edwards, D.B. 2018. Deceptive nest defence in ground-nesting birds and the risk of intermediate strategies. *PLoS ONE* 13: e0205236.

Swennen, C. 1968. Nest protection of Eider ducks and Shovelers by means of faeces. *Ardea* 56: 248–258.

The jamovi Project. 2024. *jamovi*. (Version 2.6) [Computer Software]. Retrieved from https://www.jamovi.org.

Townsend, G.H. 1966. A study of waterfowl nesting on the Saskatchewan River Delta. *Canadian Field Naturalist* 80: 74–88.

Trivers, R.L. 1972. Parental investment and sexual selection. *In* B. Campbell (ed.), *Sexual Selection and the Descent of Man*, pp. 136–179. Aldine, Chicago, USA.

Vakili, F.S., Pöysä, H., Liehrmann, O., Runko, P., Björkman, S. & Arzel, C. 2025. The older the bolder: Common Goldeneye antipredator behaviour based on long-term individual data. *Animal Behaviour* 220: 123046.

Valverde, J.A. 1960. Vertebrados de las marismas del Guadalquivir. (Introducción a su estudio ecológico). *Archivos del Instituto de Aclimatación de Almería* 9: 1–168.