

Factors affecting flushing distance in incubating female greylag geese *Anser anser*

Tomasz S. Osiejuk & Lechosław Kuczyński

Osiejuk, T.S. & Kuczyński, L. 2007: Factors affecting flushing distance in incubating female greylag geese *Anser anser*. - Wildl. Biol. 13: 11-18

We studied risk-taking behaviour of breeding greylag geese *Anser anser* in western Poland. Our objectives were to test predictions resulting from the parental investment theory by observing variation in flushing distance for incubating females in relation to clutch size, stage of incubation, nest type and number of human visits to the nests. We found that the best predictor of flushing distance was the stage of breeding; a negative relationship was observed between the number of incubation days and the observed flushing distance. Hence, females showed more risky behaviour (shortening their flushing distance) in clutches with a higher probability of hatching, i.e. in agreement with the parental investment theory. We found only a small effect of clutch size in relation to flushing distance and not in the direction expected from the parental investment theory, i.e. females incubating the largest clutches demonstrated the largest escape distance. This finding may be due to unknown age and experience of particular females which, at least potentially, may underlie the observed variation in flushing distance. We also found that females adjusted their flushing distance depending on nest location and potentially different concealment. We found no effect of repeated human visits. Flushing distance was nearly significantly shorter in unsuccessful females (whose nests were later destroyed) than in successful females. Hypotheses explaining risk-taking differentiation patterns in greylag geese are discussed. Our findings suggest that using exclusively flushing distance (or another single behavioural measure of response to human disturbance) might be misleading and should be used carefully for managing access to wildlife areas.

Key words: *Anser anser*, flushing distance, greylag goose, parental investment, risk-taking behaviour

Tomasz S. Osiejuk, Department of Behavioural Ecology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland - e-mail: osiejuk@amu.edu.pl

Lechosław Kuczyński, Department of Avian Biology & Ecology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland - e-mail: lechu@amu.edu.pl

Corresponding author: Tomasz S. Osiejuk

Received 30 May 2005, accepted 28 December 2005

Associate Editor: Jesper Madsen

Analysis of the evolution of sexual strategies in terms of 'parental investment' has led biologists to conclude that organisms face two fundamental decisions about reproduction. The first trade-off concerns spending resources on reproduction vs spending them on growth and survival. The second trade-off is related to the problem of resource allocation among the offspring (Clutton-Brock & Godfray 1991, Stearns 1992). There are several parameters underlying variation in parental investment patterns both within and between species. The relative reproductive value of offspring (Pressley 1981, Regelman & Curio 1983, Montgomerie & Weatherhead 1988, Bruun et al. 1997) and predation risk to parents are known to have major effects on decisions related to investment (e.g. Bruun et al. 1997; for a review see Lima & Dill 1990).

Plenty of strategies are applied by animals to avoid predators, varying from camouflage and remaining motionless through aposematism to escape and self-defence (Lima & Dill 1990, Krebs & Davies 1993, Laursen et al. 2005). Incubating bird females constitute a special case of predator-prey interaction because an approaching predator poses a threat to both parent and offspring. In cryptically coloured birds, the decision to escape from a clutch may involve the cost of immediate advertising the nest location to the predator and subsequent loss of the current reproduction attempt. Therefore, incubating parents face a serious decision problem, and at least theoretically they may employ two alternative strategies: 1) escape or 2) rely on their own camouflage and remain motionless (Lima & Dill 1990). Alternatively, we may ask how long a parent may delay flushing from its nest, and how this delay (or flushing distance) is balanced between the direct risk to the parent and the risk of revealing the nest position (Albrecht & Klvaňa 2004). Therefore, measurements of flushing distances from an approaching researcher may be used as an appropriate measure of parental investment in cryptically coloured birds (Forbes et al. 1994, Burhans & Thompson 2001, Albrecht & Klvaňa 2004). In this paper, we focused on factors affecting the escape behaviour of incubating female greylag geese *Anser anser* approached by a human being.

Several potential factors may affect the escape decision in the greylag goose. Based on the parental investment theory (Wallin 1987), we may expect that incubating female greylag geese should be more willing to take a risk (i.e. stay longer at the nest) with increasing clutch size (i.e. with a higher reproductive value of the clutch). In greylag geese, adult mortality during incubation is low, whereas losses due to egg

predation may be substantial (Witkowski 1983, Osiejuk 1998). Therefore, our second prediction is that the closer to hatching, the greater the probability of survival of the offspring. Thus, during incubation there will be a decrease in the ratio of parental to offspring survival until the next reproductive season (Andersson et al. 1980, Redondo 1989).

The escape decision of incubating birds may also rely on nest location, as vegetation and other factors may strongly affect the probability of clutch and/or female detection by predators. However, there is still little information on how vegetation camouflage affects flushing distance, and how different aspects of nest site are perceived by incubating females as protective (Burhans & Thomson 2001, Albrecht & Klvaňa 2004). Human visits to bird nests may result in positive reinforcement or habituation. Positive reinforcement may occur if the parent and the offspring are left unharmed after visits (Knight & Temple 1986b). Positive reinforcement results in an inflation of the parent's perception of its own capacity; therefore, the risk-taking should increase. This could lead to erroneous conclusions about time effect on nest defence (Knight & Temple 1986a). Alternatively, habituation to visits by human beings could result in a lower probability of parents attacking an intruder (Knight et al. 1987). Both habituation and/or positive reinforcement, however, are expected to result in females remaining in the incubation posture on approach.

The objectives in our study were to evaluate how escape decisions in the incubating female greylag geese are affected by: 1) clutch size, 2) stage of incubation, 3) nest type and its surroundings, and 4) number of human visits to the nest. Especially, we tested how flushing-distance variation fits the predictions of the parental investment theory. In this paper, we also discuss how this behaviour could be indicative for estimating human disturbance on greylag goose populations.

Methods

Study area

The study was carried out in a flooded area at the confluence of the Warta and the Odra rivers in western Poland (Ujście Warty National Park; 52°34'N, 14°53'E). The reservoir covers an area of about 5,000 ha and is bordered by dikes. During the study period (spring 1994-1996), the water level was high and the area resembled a shallow lake with islands of willow bushes and willow trees *Salix* spp. Only in June

1995 the water level was low enough to change the dominant landscape to meadows and pastures (for more details see Osiejuk et al. 1999). The dominant vegetation surrounding goose nests were willow bushes (diameter: 10–40 m, height: 2–4 m), old willow trees (up to 15 m high) and rows of young willow trees (height: 5–8 m). The dominant feature of the area is the unpredictable variation in water level which could modify nesting conditions both between and within seasons.

Potential predators of greylag goose nests were hooded crow *Corvus corone*, magpie *Pica pica*, red fox *Vulpes vulpes*, wild pig *Sus scrofa*, pine marten *Martes martes*, stone marten *Martes foina* and American mink *Mustela vison* (Majewski 1986, Osiejuk 1998, Bartoszewicz & Zalewski 2003).

Measurements of flushing distance

The study was conducted during the breeding seasons of 1994–1996. Between one and five visits were made per nest each year. Successive visits were quantified.

Greylag goose nests were approached by two people in a boat with an electric or a silent gas engine. When the female left the nest, the distance between the nest and the boat (DIST) was estimated to the nearest 1 m. The distribution of flushing distance was highly skewed and significantly different from a normal distribution (Kolmogorov-Smirnov: $Z = 2.55$, $P < 0.001$). Thus, we transformed DIST, and for all tests we used the following index of flushing distance: $\text{LOGDIST} = \log(\text{DIST})$. LOGDIST is symmetrically distributed and does not deviate from the normal distribution (Kolmogorov-Smirnov: $Z = 1.30$, $P > 0.05$). All statistical tests were performed using LOGDIST, but to make its values meaningful, corresponding values of flushing distance (\pm SE) were also given in text and figures. There was no year effect on flushing distance ($F_{2,134} = 0.953$, $P = 0.388$), so all data were pooled before analysis.

Factors affecting flushing distance

The number of eggs in the nests was counted at each visit. For analysis of variance, clutch sizes were pooled in three classes (variable CLUTCH-SIZE: 2–4, 5–6, and > 6 eggs).

Actual hatching dates were known in 40 of 97 cases. In the remaining 57 cases, we estimated the remaining incubation time and hatching date on the basis of egg density and water test (Westerkov 1950, Osiejuk 1998). All eggs were measured and numbered with a marker when first found, and they were weighed and tested in water at each visit. The methods were

developed as a part of a more extensive study in the Słońsk Reserve (1994–1996) during which 206 breeding pairs were investigated. The accuracy (mean deviation in days) of our clutch ageing method was 1.6 ± 1.9 days (Osiejuk 1998).

We noted three variables describing nest type and nest surroundings: 1) OVER-WATER: nest height above the water level (0 vs > 0 m); 2) VEGETATION: vegetation height above the nest (< 4.5 m vs ≥ 4.5 m); and 3) TO-OPEN-WATER: distance from the nest to open water (< 3 m vs ≥ 3 m). Median values were used as criteria for the above divisions. A nesting attempt was considered successful if at least one of the goslings survived to the time of leaving the nest.

During the nest surveys, we also measured temperature, time of day and wind speed. Preliminary investigations showed no significant influence of the variables on flushing distance, so they are not presented in this paper. Similar results were obtained by Gunness & Weatherhead (2002) who studied three duck species.

Statistical approach

General Linear Models (GLM) and model notation were applied mainly according to Grafen & Hails (2002). Statistics were calculated using MiniTab 13 (Ryan & Joiner 2001) and SPSS 10 software (Norušis 2000), and P values are two-tailed, unless stated otherwise.

Results

Material collected

We collected data from 97 greylag goose nests (29 nests in 1994, 27 nests in 1995 and 41 nests in 1996). Altogether, we had 135 flushing distance observations (37 in 1994, 36 in 1995 and 62 in 1996) and the females were flushed once from 49 nests, twice from 32 nests, three times from six nests and four times from a single nest.

The number of visits we made was positively correlated with number of days of incubation ($r = 0.54$, $P < 0.001$, $N = 135$). This is not surprising as the nests that were incubated longer had a greater chance of being visited more times. However, this result leads to difficulties in testing the influence of number of visits on flushing distance for the incubating female. Therefore, we used two statistical approaches to analyse our data. First, we analysed only the earliest records, i.e. first-flushing distance measured for each nest (female), to test effects of clutch size, breeding stage and nest site. Then we used also data from re-

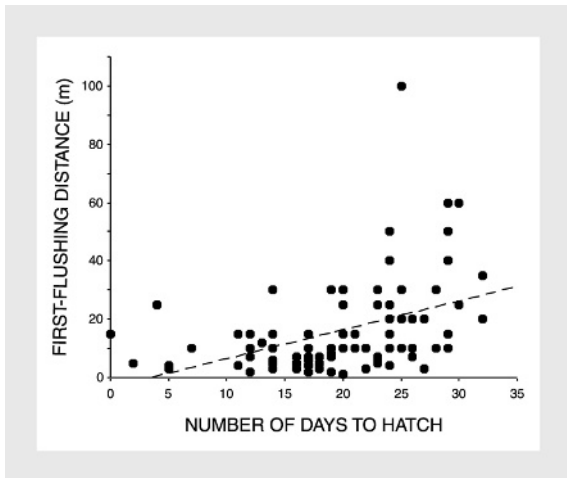


Figure 1. Relationship between first-flushing distance (in m) and time left to hatching (number of days) for incubating female greylag geese.

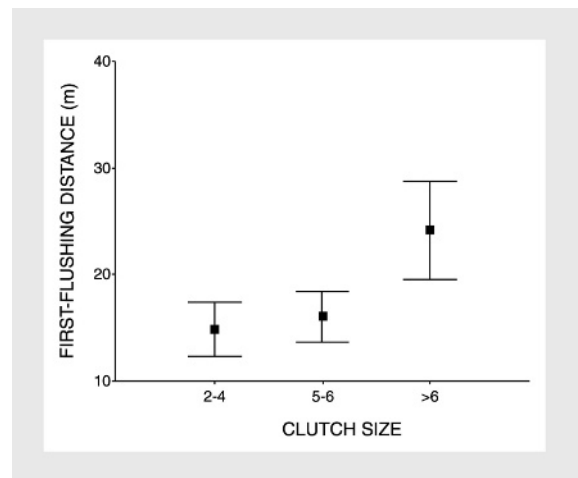


Figure 2. Relationship between mean (\pm SE) first-flushing distance (in m) and clutch size for incubating female greylag geese with different clutch size.

peated visits to analyse how incubation progress and humans affect females' decisions. This was a very conservative approach as LOGDIST was found to be independent of the number of visits to the nest ($F_{3,134} = 0.58$, $P = 0.627$).

Analysis of the first flushing attempts

First-flushing distance averaged 16.5 ± 1.60 m (range: 1-100 m, $N = 96$). We used a GLM approach to check for significant relations among a set of predictors. LOGDIST was significantly correlated with different measures of breeding stage, e.g. number of days after the first egg was laid ($r = -0.32$, $N = 96$, $P = 0.001$), and number of days since incubation was started ($r = -0.40$, $N = 96$, $P < 0.001$). We found, however, the strongest correlation between LOGDIST and number of days left to hatching ($r = 0.45$, $N = 96$, $P < 0.001$), so this variable (in the following termed TO-HATCH) was used in the models. We found that first-flushing distance depended mostly on time left to hatching, and the longer the clutch was

incubated, the longer the females stayed at the nest (Fig. 1, Table 1). We also found that large clutches (> 6 eggs) were left earlier (first-flushing: 24.1 ± 4.6 m) than medium (16.7 ± 2.5 m; Tukey adjusted: $P = 0.044$) and small clutches (14.0 ± 2.4 m; Tukey adjusted: $P = 0.030$, Fig. 2). First-flushing distance was significantly shorter in nests located in shorter vegetation, i.e. within willow bushes, than in groups of higher trees (see Table 1 and Fig. 3).

Analysis of repeated flushing attempts

Flushing distance was measured at least twice in 31 nests, and it was found to be significantly longer during the first visit (23.0 ± 3.85 m) than during the second visit (15.8 ± 3.9 m; repeated measures GLM: Wilks' Lambda = 0.828, $F_{1,30} = 6.24$, $P = 0.018$). In the next repeated measures model, we included also number of days to hatching at the first visit (TO-HATCH) and number of days that passed between the first and second visit (TSHIFT). In this case, the statistically significant factors were TO-HATCH ($F_{1,28} =$

Table 1. Results of the General Linear Model analysis on the effects of variables associated with the reproductive value of clutch and nest location variables on first-flushing distance of female greylag geese. Effect of CLUTCH SIZE was analysed using Tukey simultaneous tests. All pairwise comparisons among levels of CLUTCH SIZE were 1) 2-4, 2) 5-6, 3) > 6 eggs, and CLUTCH SIZE classes were 1 and 2 ($P = 0.994$), 1 and 3 ($P = 0.030$) and 2 and 3 ($P = 0.044$). The variable TO-HATCH is a covariate ($t = 5.08$, $P < 0.001$).

Variable	DF	Seq SS	Adj SS	Adj MS	F	P
CLUTCH SIZE	2	0.6803	0.8157	0.4078	3.64	0.030
TO-HATCH	1	2.9915	2.8911	2.8911	25.78	0.000
OVER WATER	1	0.0583	0.2080	0.2080	1.85	0.177
VEGETATION	1	0.7018	0.5954	0.5954	5.31	0.024
TO-OPEN-WATER	1	0.0107	0.0107	0.0107	0.10	0.759
Error	85	9.5306	9.5306	0.1121		
Total	91	13.9732				

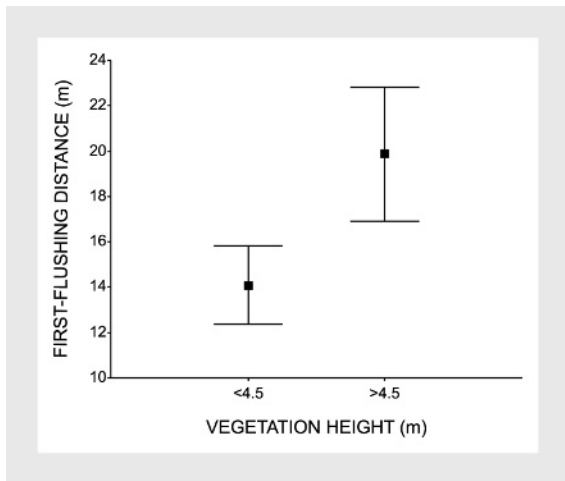


Figure 3. Relationship between mean (\pm SE) first-flushing distance (in m) and vegetation height (in m) for incubating female greylag geese.

12.31, $P = 0.002$) and TSHIFT ($F_{1,28} = 5.94$, $P = 0.021$).

We found that the longer the time between the first and second flushing attempt was, the more shortened was the second flushing distance in comparison to the first one (Spearman's rho: $r_s = -0.36$, $N = 31$, $P = 0.048$). However, this relationship was insignificant when controlled for clutch age at the first flushing attempt ($r_s = -0.32$, $N = 28$, $P = 0.081$).

Flushing distance and nesting success

First-flushing distance was close to being significantly shorter in unsuccessful females, whose nests were later destroyed, than in successful females ($F_{1,62} = 3.733$, $P = 0.058$). Mean first-flushing distance was 16.1 ± 2.4 m for unsuccessful females and 23.9 ± 4.0 m for successful ones. The difference was insignificant when TO-HATCH and CLUTCH-SIZE were included into the model.

Discussion

We focussed on four factors that are likely to affect flushing distance (reflecting the willingness of a female to take a risk) in greylag geese. These factors include: clutch size, breeding stage, nest site and human visits. We found only a small effect of clutch size on the escape decision, and the effect found was not in the direction expected from the parental investment theory. We found that the best predictor of flushing distance was the stage of breeding, measured as the

number of days left to hatching. The willingness to take a risk (shortening the flushing-distance) was negatively correlated with the time left to hatching. We also found some evidence that females adjust their flushing distance in relation to nest location and potentially different concealment. There was no positive reinforcement or habituation due to repeated visits.

Effect of clutch size

The parental investment theory predicts that females should invest more for offspring of a higher reproductive value (Trivers 1972, Montgomerie & Weatherhead 1988). Regarding clutch size, one may therefore expect that females with larger clutches should exhibit shorter flushing distances than females at the same breeding stage but with smaller clutches. We found that females incubating the largest clutches flushed from significantly longer distances than females having smaller clutches. The analysis involved full clutches with time of incubation and nest location included in the model. So, the observed behaviour seems to contrast the parental investment theory and some other studies on precocial species (Forsslund & Larsson 1992, Forbes et al. 1994, Sjöberg 1994). This unexpected increase in risk-taking with decreasing clutch sizes might result from many reasons, e.g. unknown population age structure and female condition or experience. Waterfowl have been reported to respond to manipulation of clutch size and appear to be able to judge the value of their clutch (Armstrong & Robertson 1988, Sjöberg 1994). Therefore, individual clutch value, adjusted for several possible factors such as age, female condition and food availability, may be a better measure of parental investment for testing a nest defence hypothesis than the simple clutch size variable.

How can this 'experience adjustment' work? For example, older geese usually lay larger clutches and/or larger eggs than younger geese (e.g. Hamann & Cooke 1987, Robertson et al. 1994, Woog 2002). In general, reproduction is known to be age-specific in geese and ducks (Finney & Cooke 1978, Raveling 1981, Blum et al. 1997, Kampp & Preuss 2005). Therefore, we may expect that older females are more experienced and that vigilance in such birds is more effective than in younger females. So, older females may faster recognise a potential danger, may faster cover the eggs with down feathers, and therefore may be able to leave the nest earlier than inexperienced females. Such a behaviour could be advantageous, as the covering of eggs protects them against cold for quite a long time, while

simultaneously the longer flushing distance hinders nest localisation by a potential predator and enables females to avoid risking their own lives. The lack of experience in nest defence is, for example, a reason for lower reproductive success rates in first-time breeders of snow geese *Anas caerulescens* (Cooke et al. 1995). In general, many researchers stress the importance of age-related skills for reproductive success in geese (e.g. Forslund & Larsson 1992, Rockwell et al. 1993). Moreover, a recent study on turnstones *Arenaria interpres* demonstrated experimentally that birds may change their response depending on their individual state independently of the strength of the disturbance by humans (Beale & Monaghan 2004a).

Stage of incubation

The best predictor of flushing distance in greylag geese was the time left to hatching. Our observations indicate that during the first half of incubation females tend to leave the nest quite early and change their behaviour at the final stage of incubation. However, it is noteworthy that the shortest flushing distances observed are still long enough to enable a safe escape. We know of only a single example of a female goose bitten to death on the nest by a fox during the three years of our field research (Osiejuk 1998). However, many times we found completely destroyed nests, proving that a relatively strong and potentially dangerous predator was active in the area. This part of our results is in agreement with the parental investment theory, as females were found to invest more in eggs with a higher probability of hatching (Osiejuk 1998), i.e. offspring with a higher reproductive value (Trivers 1972, Montgomerie & Weatherhead 1988). Previous studies on various duck and goose species have shown results consistent with our research, i.e. females tend to wait longer before flushing as incubation progresses (Mallory & Weatherhead 1993, Forbes et al. 1994, Sjöberg 1994, Albrecht & Klvaňa 2004). Moreover, Albrecht & Klvaňa (2004) have shown that incubating mallards *Anas platyrhynchos* were extremely attentive to the nest during the last part of the incubation stage, similarly to our goose species. Escape behaviour was found to be affected by offspring value also in other bird species (Dale et al. 1996) and animals from other groups, e.g. fish (Pressley 1981) or insects (Tallamy 1982).

Nest location

Nests of greylag geese in the Słońsk Reserve were located in few microhabitats which can be divided into two main classes: 1) nests in willow bushes and 2) nests

in trees. Nests in bushes were usually placed at the water level and were hidden inside the dense vegetation, invisible from a longer distance, especially when leaves appear. Nests in trees were placed above the water level, usually not concealed by dense vegetation, and consequently they were visible from a distance throughout the breeding season. Earlier research showed that these two nest types differed in overall breeding success, but this was mainly because nests in trees did not suffer from floods, typical for our study area (Osiejuk 1998). In our study we found that flushing distance was shorter for nests well concealed in bushes. This result suggests that female behaviour is adjusted to nest site location. Females appear to distinguish properly between visible and hidden nests and delay flushing when they 'expect' to remain unobserved. This also supports our earlier hypothesis that female experience may play an important role in shaping variation of flushing distance. Corresponding results were reported also by Albrecht & Klvaňa (2004), who suggested that vegetation may act as a protective cover for incubating females in mallards. Consequently, that ability to delay flushes in cryptically coloured birds may be regarded as an antipredator strategy to reduce nest advertising. Albrecht & Klvaňa (2004) also suggested that such behaviour may depend strongly on predator types presented (e.g. visually vs chemically oriented) and in some cases may be maladaptive. In our case, we found that step-like differences in nest concealment (within a bush vs in a tree) may affect a female's nest defence strategy. Similarly to the mallard, an escape decision seems to be balanced by cryptic colouration (Albrecht & Klvaňa 2004), rather than by reduced locomotory abilities (e.g. Cuadrado et al. 2001, Cooper 2003). Anyway, many studies confirm that geese in particular are able to adjust their behaviour to the current predator pressure. For example, Forslund (1993) demonstrated that vigilance behaviour of barnacle geese *Branta leucopsis* depends not only on brood size, but also is adjusted to predator abundance. Kahlert (2003) showed that the choice of moult site in wing-moulting greylag geese is mainly affected by predation risk and level of disturbance, which also indicates a high predation-risk perception in this species.

Effect of repeated visits

We found that geese escaped later closer to hatching, regardless of the number of visits, and hence no positive reinforcement or habituation effect of repeated flushes was observed. Sjöberg (1994) obtained similar results for Canada geese *Branta canadensis*, and

Forbes et al. (1994) did so for different duck species. Thus, the increased defence intensity during incubation was attributed exclusively to an increased reproductive value of the clutch (Andersson et al. 1980, Redondo 1989, Sjöberg 1994).

Conclusions

We found that the most important factor affecting escape decisions in female greylag geese was the advancement of clutch incubation. In other words, females correctly evaluate the increasing reproductive value of the clutch as incubation is progressing. On the other hand, our results suggest that clutch size in long-lived, precocial birds may not be an appropriate measure of the reproductive value of their clutch. It seems to be essential to take into account the age-related characteristics of females (e.g. experience) and some environmental factors (e.g. nest concealment), which might be crucial for escape decision making. Our results support recent opinions that behavioural responses are perhaps not the best measure of how bird populations are disturbed by humans (Gill et al. 2001, Beale & Monaghan 2004a, b). This means that some practical conservation priorities (e.g. managing access to nesting areas) need to be re-established as the direct links between population disturbance and simple measures of behavioural response to human presence may be misleading.

Completely denying access to some areas is often not feasible, but keeping a safe distance between potential human intruders and nesting geese, which prevent them from leaving their nests, seems to be a reasonable recommendation. The necessary width of protection zones around the nesting areas should be larger than the maximal escape distance measured for the whole breeding period. We expect that such a management priority would not only decrease the number of disturbances, but also increase the hatching success because egg losses by predation would be reduced (as for example in grebes; Keller 1989).

Acknowledgements - funding for this study was provided through the Polish-German Foundation (Stiftung für deutsch-polnische Zusammenarbeit), project no. 4722/93. Tomasz S. Osiejuk was supported by a scholarship at Université Paris Sud by the Foundation for the Polish Science. We would like to thank Professor Czesław Błaszak for his invitation to join this project, Jacek Engel for providing valuable technical help during the project and two anonymous referees for their comments on an earlier version of this paper.

References

- Albrecht, T. & Klvaňa, P. 2004: Nest Crypsis, Reproductive Value of a Clutch and Escape Decisions in Incubating Female Mallards *Anas platyrhynchos*. - *Ethology* 110: 603-613.
- Andersson, M., Wiklund, C.G. & Rundgren, H. 1980: Parental defence of offspring: a model and an example. - *Animal Behaviour* 28: 536-542.
- Armstrong, T. & Robertson, R.R. 1988: Parental investment based on clutch value: Nest desertion in response to partial clutch loss in dabbling ducks. - *Animal Behaviour* 36: 941-943.
- Bartoszewicz, M. & Zalewski, A. 2003: American mink, *Mustela vison* diet and predation on waterfowl in the Slonsk Reserve, western Poland. - *Folia Zoologica* 52: 225-238.
- Beale, C.M. & Monaghan, P. 2004a: Behavioural responses to human disturbance: a matter of choice? - *Animal Behaviour* 68: 1065-1069.
- Beale, C.M. & Monaghan, P. 2004b: Human disturbance: people as predation-free predators? - *Journal of Applied Ecology* 41: 335-343.
- Blums, P., Hepp, G.R. & Mednis, A. 1997: Age-specific reproduction in three species of European ducks. - *Auk* 114: 737-747.
- Bruun, M., Sandell, M.I. & Smith, H.G. 1997: Polygynous male starlings allocate parental care effort according to relative hatching date. - *Animal Behaviour* 54: 73-79.
- Burhans, D.E. & Thompson, F.R., Jr. 2001: Relation of songbird nest concealment to nest fate and flushing behaviour of adults. - *Auk* 118: 237-242.
- Clutton-Brock, T. & Godfray, C. 1991: Parental investment. - In: Krebs, J.R. & Davies, N.B. (Eds.); *Behavioural Ecology. An Evolutionary Approach*, 3rd edition. Blackwell Scientific Publications, Oxford, pp. 234-262.
- Cooke, F., Rockwell, R.F. & Land, D.B. 1995: The Snow Geese of La Pérouse Bay: natural selection in the wild. - Oxford, 289 pp.
- Cooper, W.E. 2003: Effect of Risk on Aspects of Escape Behaviour by Lizard, *Holbrookia propinqua*, in Relation to Optimal Escape Theory. - *Ethology* 109: 617-626.
- Cuadrado, M., Martín, J. & López, P. 2001: Camouflage and escape decisions in the common chameleon *Chamaeleo chamaeleon*. - *Biological Journal of Linnean Society* 72: 547-554.
- Dale, S., Gustavsen, R. & Slagsvold, T. 1996: Risk taking during parental care: a test of three hypotheses applied to the pied flycatcher. - *Behavioural Ecology & Sociobiology* 39: 31-42.
- Finney, G. & Cooke, F. 1978: Reproductive habits of the snow geese: the influence of female age. - *Condor* 80: 147-158.
- 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. - *Behavioural Ecology & Sociobiology* 34: 79-85.

- Forslund, P. 1993: Vigilance in relation to brood size and predator abundance in the barnacle goose, *Branta leucopsis*. - *Animal Behaviour* 45: 965-973.
- Forslund, P. & Larsson, K. 1992: Age-related reproductive success in the Barnacle Goose. - *Journal of Animal Ecology* 61: 195-204.
- Gill, J.A., Norris, K. & Sutherland, W.J. 2001: Why behavioural responses may not reflect the population consequences of human disturbance. - *Biological Conservation* 97: 265-268.
- Grafen, A. & Hails, R. 2002: *Modern Statistics for the Life Sciences*. - Oxford University Press, Oxford, 351 pp.
- Gunness, M.A. & Weatherhead, P.J. 2002: Variation in nest defense in ducks: methodological and biological insights. - *Journal of Avian Biology* 33: 191-198.
- Hamann, J. & Cooke, F. 1987: Age effects on clutch size and laying dates of individual female Lesser Snow Geese *Anser caerulescens*. - *Ibis* 129: 527-532.
- Kahlert, J. 2003: The constraint on habitat use in wing-moulting Greylag Geese *Anser anser* caused by anti-predator displacements. - *Ibis* 145: E45-E52.
- Kampp, K. & Preuss, N.O. 2005: The Greylag Geese of Utterslev Mose - A long-term population study of wild geese in an urban setting. - *Dansk Ornithologisk Forenings Tidsskrift* 99: 1-78.
- Keller, V. 1989: Variations in the response of Great Crested Grebes *Podiceps cristatus* to human disturbance - a sign of adaptation? - *Biological Conservation* 49: 31-45.
- Knight, R.L., Grout, D.J. & Temple, S.A. 1987: Nest-defence behavior of the American Crow in urban and rural areas. - *Condor* 89: 175-177.
- Knight, R.L. & Temple, S.A. 1986a: Methodological problems in studies of avian nest defence. - *Animal Behaviour* 34: 561-566.
- Knight, R.L. & Temple, S.A. 1986b: Why does intensity of avian nest defence increase during the nesting cycle? - *Auk* 103: 318-327.
- Krebs, J.R. & Davies, N.B. 1993: *An Introduction to Behavioural Ecology*, 3rd edition. - Blackwell Scientific Publications, Oxford, 420 pp.
- Laursen, K., Kahlert, J. & Frikke, J. 2005: Factors affecting escape distances of staging waterbirds. - *Wildlife Biology* 11: 13-19.
- Lima, S.L. & Dill, L.M. 1990: Behavioral decisions made under the risk of predation - a review and prospectus. - *Canadian Journal of Zoology* 68: 619-640.
- Majewski, P. 1986: Breeding ecology of the Mallard on the flooded area of the Warta river mouth, Poland. - *Wildfowl* 37: 88-103.
- Mallory, M.L. & Weatherhead, P.J. 1993: Observer effects on common goldeneye nest defence. - *Condor* 95: 467-469.
- Montgomerie, M.L. & Weatherhead, P.J. 1988: Risk and rewards of nest defence by parent birds. - *Quarterly Review of Biology* 63: 167-187.
- Norušis, M.J. 2000: *SPSS 10.0 Guide to Data Analysis*. - Prentice-Hall, 577 pp.
- Osiejuk, T.S. 1998: Breeding biology of Greylag Goose *Anser anser* in varying condition of Słońsk reserve. - Unpubl. PhD thesis, Adam Mickiewicz University, Poland, 119 pp.
- Osiejuk, T.S., Kuczyński, L., Jermaczek, A. & Tryjanowski, P. 1999: The effect of water conditions on breeding bird communities of pastures, meadows and shrub habitats in the Słońsk reserve, NW Poland. - *Biologia, Bratislava* 54: 207-214.
- Pressley, P.H. 1981: Parental effort and the evolution of nest-guarding tactics in the treespine stickleback, *Gasterosteus aculeatus* L. - *Evolution* 35: 282-295.
- Raveling, D.G. 1981: Survival, experience and age in relation to breeding success of Canada geese. - *Journal of Wildlife Management* 45: 817-829.
- Redondo, T. 1989: Avian nest defence: Theoretical models and evidence. - *Behaviour* 111: 161-195.
- Regelmann, K. & Curio, E. 1983: Determinants of brood defence in the great tit *Parus major* L. - *Behavioural Ecology & Sociobiology* 13: 131-145.
- Robertson, G.J., Cooch, E.G., Lank, D.B., Rockwell, R.F. & Cooke, F. 1994: Female age and egg size in the Lesser Snow Goose. - *Journal of Avian Biology* 25: 149-155.
- Rockwell, R.F., Cooch, E.G., Thompson, C.B. & Cooke, F. 1993: Age and reproductive success in female lesser snow geese: experience, senescence, and the cost of philopatry. - *Journal of Animal Ecology* 62: 323-333.
- Ryan, B.F. & Joiner, B.L. 2001: *Minitab handbook*, 4th edition. - Pacific Grove, Duxbury Press, 379 pp.
- Sjöberg, G. 1994: Factors affecting nest defence in female Canada Geese *Branta canadensis*. - *Ibis* 136: 129-135.
- Stearns, S.C. 1992: *The Evolution of Life Histories*. - Oxford University Press, 248 pp.
- Tallamy, D.W. 1982: Age-specific maternal defence in *Gargaphia solani* (Hemiptera: Tingidae). - *Behavioural Ecology & Sociobiology* 11: 7-11.
- Trivers, R.L. 1972: Parental investment and sexual selection. - In: Campbell, B. (Ed.); *Sexual Selection and the Descent of Man, 1871-1971*. Heinemann, London, pp. 136-179.
- Wallin, K. 1987: Defence as parental care in Tawny Owls (*Strix aluco*). - *Behaviour* 102: 213-230.
- Westerkov, K. 1950: Methods for determining the age of game bird eggs. - *Journal of Wildlife Management* 14: 56-67.
- Witkowski, J. 1983: Population studies of the Greylag goose *Anser anser* breeding in the Barycz Valley, Poland. - *Acta Ornithologica* 19: 179-216.
- Woog, F. 2002: Reproductive success and pairing in Hawaiian Geese (*Branta sandvicensis*) in relation to age and body size. - *Journal für Ornithologie* 143: 43-50.