

Clutch desertion in Barrow's goldeneyes (*Bucephala islandica*) — effects of non-natal eggs, the environment and host female characteristics

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Addition of eggs to nests of conspecifics is a common avian alternative breeding strategy, called conspecific brood parasitism. The consequences of this breeding strategy on recipient breeding success have seldom been quantified, while taking into account environmental factors and host female characteristics. We study the occurrence of nest parasitism and, using an information theoretic approach, the most important factors responsible for nest desertion in female Barrow's goldeneyes (*Bucephala islandica*). Nest parasitism is common in the study population, and 58% of the nests contained non-natal eggs, representing 20% of all eggs. A prime factor explaining nest desertion was the number of non-natal eggs. There were also significant effects of year and own clutch size. By contrast, ambient temperature and female laying date did not influence nest desertion. These results provide one of the first demonstrations that non-natal eggs can have substantial negative effects also in precocial species.

Introduction

In egg-laying animals such as fishes, insects and birds, addition of eggs to clutches of conspecifics is a common alternative reproductive strategy, usually termed conspecific or intraspecific brood parasitism or egg dumping (Eadie *et al.* 1988, Yom-Tov 2001, Åhlund & Andersson 2001, Loeb 2003). Whereas advances in molecular techniques are drawing attention to complex facets of this behaviour, such as relatedness among

egg donors and recipients, many basic aspects of nest parasitism remain insufficiently clarified. In particular, the effects of donor eggs on the fitness of recipients (e.g. Eadie & Fryxell 1992, Brown & Brown 1999, Lyon 2003, Pöysä 2004) may be crucial and need further study. Quantifying the costs and benefits of single and joint breeding forms an integral, yet underappreciated (e.g. Aviles *et al.* 2004), part of assessing the potential role of kin selection in nest parasitism, and the evolution of nest parasitism in general.

As waterfowl are typically precocial and do not care for the young in the nest, and as their main parental care after hatching is escorting young to feeding sites and antipredatory vigilance (Öst *et al.* 2007), nest parasitism has been considered to be of negligible cost (e.g. Larsson *et al.* 1995), or even beneficial to hosts (e.g. Lepage *et al.* 1998). Although incubating larger clutches entails energetic costs (e.g. Erikstad & Tveraa 1995), there is little direct evidence demonstrating costs of nest parasitism in waterfowl (Eadie 1989) and the results are mostly indicative. One reason for the absence of negative effects may be that previous studies focused mainly on post-hatch brood amalgamation, whereas negative effects of nest parasitism might manifest themselves during incubation, the cost of which has until recently been considered negligible as compared with that of nestling care (Monaghan & Nager 1997, de Heij *et al.* 2006). Clutch enlargement by nest parasitism, however, may impose a higher physiological strain on parents, which in turn may affect their parental investment decisions (de Heij *et al.* 2006).

Abandoning offspring negatively affects their survival (Eadie & Lyon 1998), and in the case of nest desertion, egg survival probability invariably approaches zero. From the parent's perspective, abandonment can be a way of avoiding unacceptably high costs of reproduction in relation to projected payoffs (Pöysä *et al.* 1997, Eadie & Lyon 1998). Theory predicts offspring abandonment to be beneficial when current reproduction is outweighed by its costs, scaled to the residual reproductive value of the individual (Clark & Ydenberg 1990, Stearns & Kawecki 1994, Székely *et al.* 1996). The expected benefit of nest desertion is generally higher in long-lived animals, and thus life-history characteristics such as longevity will affect the cost/benefit ratio of aborting the current breeding attempt.

Depending on their state, incubating females may lack sufficient nutrient reserves (Blums *et al.* 1997) or experience (Ardia & Clotfelter 2007) to successfully complete incubation, or they may be unable to adjust their clutch size in the face of nest parasitism, and therefore end up in an unfavourable situation. If the enlarged clutch imposes too great costs in relation to its potential fitness benefits, the incubating female

may favour her own future survival and reproduction over investment in current reproduction (Williams 1966) by deserting the clutch.

The objective of this study is to determine the occurrence of nest parasitism and its effects on nesting success of egg recipients. We examine the relative importance of non-natal eggs, environmental conditions and female characteristics on the recipient's probability of successfully incubating her clutch. We use a population of a cavity nesting duck, the Barrow's goldeneye (*Bucephala islandica*), a species with frequent nest parasitism (Eadie 1989, Eadie & Fryxell 1992), as our study system.

Material and methods

Study area and female data

The study was conducted at Riske Creek, close to the town of Williams Lake (51°52'N, 122°21'W), British Columbia, Canada, during the breeding seasons of 2005 and 2006. The study area consisted of a 15 × 15 km prairie plateau interspersed with a large number of ponds and lakes with trembling aspen (*Populus tremuloides*) stands along the shores. Immediately prior to the breeding season of 2004, nest boxes were erected in the aspen and coniferous stands, as close to the shorelines of the wetlands as possible, resulting in a total of 36 ponds and lakes bearing a total of 127 nest boxes. A minority of these 127 nest boxes were older ones present from previous nest box programmes. The new nest boxes were occupied from 2004 onwards. During the breeding season of 2005, 68 out of 127 nest boxes (53.5%) were occupied, and in 2006, 71 out of 127 (55.9%). This suggests that the population was not nest-site limited.

We collected data on female age and body condition at capture. Individual ages were calculated from ringing data obtained from the current study as well as from earlier ones (ringing of Barrow's goldeneyes has been going on in the area since the early 1980s) (e.g. Evans 2003). Females found not to be ringed were regarded as two-year-olds. The ages of repeatedly observed females was estimated as: focal year of capture – (year of ringing – 2). A breeding female ringed

in 2004 would thus be regarded as four years old in 2006. We use minimum age estimates in our analysis. Birds were weighed on a spring balance to the nearest 10 g, and the length of their tarsus was measured to the nearest 1 mm with a vernier calliper. Condition indices were calculated as standardized residuals of actual body weights from those predicted by regressions of body weight on tarsus length. All females were caught during the last week of incubation. Thus, female weights are directly comparable, alleviating the need to correct for potential weight loss over incubation time. Standardized residual weights were derived separately for each year.

Identifying non-natal eggs

In order to determine the occurrence of nest parasitism, we identified the origin of eggs in 99 active nests, by collecting egg albumen samples from 1098 eggs during May and June 2005 and 2006. These nests represented the majority (71.2%) of the nests initiated in the population during 2005 and 2006 (total for both years = 139). We were unable to sample all active nests due to predation during the laying period prior to sampling. The samples were collected by drilling a small (~1 mm) hole in the egg shell at the narrow end, about 10 mm from the tip of the egg. Using a syringe, we extracted a minute sample of egg albumen (~0.3 ml) (Andersson & Åhlund 2000, Andersson & Åhlund 2001, Waldeck *et al.* 2004). After withdrawing the sample, the hole was sealed using cyanoacrylate glue (Loctite® 795) in combination with accelerator (Loctite® 7455), which made the glue harden nearly immediately. This method has previously been shown not to affect the hatchability of the eggs (Andersson & Åhlund 2000, Andersson & Åhlund 2001, Waldeck *et al.* 2004). We confirmed this by comparing the proportion of hatched eggs in sampled (0.93) and unsampled eggs (0.88), using a proportions test ($\chi^2_1 = 3.38$, difference in proportions between groups = 0.05 ± 0.06 95%CI). The unsampled eggs represent clutches found too late (ca. 2 days) in the host's incubation period, when albumen becomes difficult to extract and is easily contaminated with yolk (Waldeck *et al.* 2004), and which therefore

could not be sampled. These clutches were in all other respects comparable to the sampled eggs. The eggs were then marked and measured before returning them to the nest. The albumen samples were stored in -20°C for approximately 6 months until electrophoresis.

The electrophoretic analysis of the samples was done by isoelectric focusing over a fixed pH gradient in polyacrylamide gels. This technique produces distinct band patterns, which usually vary among females and reflect genetic differences between them (Andersson & Åhlund 2001, Waldeck *et al.* 2004). The albumen samples were mainly run on one type of gel (Amersham Pharmacia Biotech, Immobiline DryPlates pH 4–7) as no further variation in band patterns was found using other gel types (Amersham Pharmacia Biotech, Immobiline DryPlates pH 4.2–4.9, pH 4.5–5.4, pH 5–6). The gels were rehydrated for 2–4 hours according to the recipe used by Waldeck *et al.* (2004). These authors give further details of the technique (*see also* Andersson & Åhlund 2001). Electrophoreses were done using Amersham Pharmacia Biotech Multiphor II System and power supply EPS 3501, and using a cooling temperature of 10°C at 3000 V, 1 mA and maximum power of 3 W.

The non-natal eggs detected using this technique differed from the natal eggs on average (\pm 95%CI) by 1.8 (\pm 0.22) bands, ranging from one to seven. Variability in protein bands was sufficient for identifying many but not all non-natal eggs (*see below*). By comparing the female-specific band patterns, we can therefore provide a conservative estimate of the number of non-natal eggs in the nests.

Nest parasitism and nest fate

Eggs with the most frequent band pattern in a nest were assumed to be laid by the recipient (*cf.* Andersson & Åhlund 2000), and band patterns differing from that of recipient eggs indicated that such eggs were laid by donor female(s). The number of eggs with other band patterns was usually considerably lower than that of the most common band pattern. In one case, the donor and recipient laid equally many eggs, leaving donor–recipient identity unclear but inconsequential.

We visited nests on average (\pm SD) 6.3 times (\pm 3.3) during the incubation period (about 32 days for successful nests), and documented occupancy. We avoided as far as possible flushing the female off the nest, but some disturbance was unavoidable, and females were flushed on average (\pm SD) 3.3 (\pm 2.0) times.

Of all the 70 nests where incubation was initiated, successful nests had a slightly higher frequency of investigator visits ($t = 3.25$, $df = 68$, mean difference = 0.07 visits per day \pm 0.04 95%CI). This difference in the frequency of nest visits is a by-product of successful nests being repeatedly visited close to hatching in order to capture the brood for marking and other work. To investigate potential bias related to length of incubation and higher brood reproductive value close to hatching, we made a bootstrap analysis of deserted and successful nests. This allowed an unbiased comparison of the number of nest visits for corresponding stages of the incubation period. For each of the 16 deserted nests, we recorded the time (in days d from incubation onset) at which the nest was found to be deserted, and recorded how many investigator visits had been made to the nest prior to the one when desertion was recorded. We then used the empirical distribution of desertion record days (i.e. days d for each deserted nest) to draw a random day d (with replacement) for each of the 54 successful nests, and calculated the number of investigator visits to the nests before that day.

The mean number (\pm SD) of investigator visits prior to the day d for the deserted and successful nests were 3.43 (\pm 2.4) and 4.65 (\pm 2.8), respectively. A permutation test with 10 000 repeats showed that deserted and successful nests did not differ statistically regarding the frequency of investigator visits, as the difference of 1.21 investigator visits lay within the 97.5% quantile limit of 1.45. Moreover, the difference was in the direction of fewer rather than more visits to unsuccessful nests before day d .

When a nest was found to be abandoned, we regarded the median day from the last visit to present as the date of abandonment. At this time, we also recorded the clutch size and compared it to that recorded at the last visit. No nests had received extra eggs after the last visit, so the

clutch composition had likely not changed. This observation is important, since it indicates that parasitic eggs were not added to the clutches after desertion (see Discussion). Although both common goldeneyes (*B. clangula*) and Barrow's goldeneyes have been found to lay eggs into inactive nests (Eadie 1989, Pöysä 2003a, 2003b), one possible explanation for our observation is that the nests were deserted so late in the season that parasitic laying did not occur anymore.

A nest was considered active if it contained one or more eggs during the breeding season. Nests that were not incubated or were depredated before hatching or desertion were only used for determining the occurrence of nest parasitism, and they were excluded from the clutch desertion analysis. In order to target only actively incubated recipient nests, we excluded nests that were not observed to have been incubated ('dump nests'), thereby also making our analysis more conservative as regards estimated negative effects of parasitism on nesting success. The onset of incubation verifies female breeding intention in the focal nest, whereas lack of incubation leaves the intentions of laying females unclear.

Statistical analysis

For the nest desertion analysis, we pre-selected a set of putative covariates to explain variation in clutch desertion probability based on *a priori* evidence from the literature suggesting the potential influence of those covariates (Lyon 1998, Brown & Brown 1999, Engstrand & Bryant 2002, Hanssen *et al.* 2003, Dawson *et al.* 2005, Roy Nielsen *et al.* 2006, de Heij *et al.* 2006, Ardia & Clotfelter 2007, Fernandez & Reboreda 2007). The independent and joint effects, and relative importance of different factors, were analyzed with logistic regression of the binary response variable desertion (1 = deserted, 0 = hatched) as a function of different combinations of the explanatory variables (Table 1). Covariates were the number of non-natal eggs, own clutch size, date of the first laid egg, age, condition, temperature during incubation and year. The temperature parameter describes the mean of the daily minimums for

the five first days of incubation. This was chosen as a standardized measure spanning an equal time interval for all nests in the analysis (the first abandonment occurred on day six of incubation). The daily minimums were selected as they most accurately describe the time incubating females have to endure at temperatures close to or below their thermoneutral zone (Gabrielsen *et al.* 1991). Temperature data were collected at Williams Lake airport (51°52'N, 122°21'W) by Environment Canada and are available on the internet (www.climate.weatheroffice.ec.gc.ca). Our study area is located ca. 32 km from this weather station at similar elevation (ca. 900 m). Lay date was either observed as the date when the first egg was laid or calculated as follows: lay date = date of finding nest – (1.5 × own clutch size at date of finding nest), as Barrow's goldeneyes lay eggs on average every 1.5 days (Thompson 1996). The covariates own clutch size, date of the first laid egg, age and condition describe female characteristics, the number of non-natal eggs the impact of parasitism, while temperature during incubation and year represent environmental factors.

If the nest was found after the onset of incubation, the lay date was calculated by first estimating the date when incubation had started and then implementing the formula mentioned above. To estimate the date of incubation start we used the egg flotation method of Kilpi and Lindström (1997), modified to the Barrow's goldeneye's incubation period of about 32 days, providing a reliable estimate of the number of days the eggs have been incubated.

Year effects were included in all models to

account for any unexplained, year-specific variation in nest desertion rates, thereby improving the precision of parameter estimates for the remaining covariates. Because the variable year only had two levels, 2005 and 2006, it was treated as a fixed factor.

Models were built from combinations of the pre-selected covariates, each model representing a specific hypothesis. We constructed candidate models in which we included every covariate on its own to investigate the possibility of a single most important covariate. Female characteristics were described by the combination of lay date, age, condition and own clutch size. Environmental effects were described by both year and temperature during incubation, whereas non-natal eggs were described by a single covariate. To restrict the size of the model set and keep our hypotheses as simple and unambiguous as possible, we excluded interaction terms from the model set. Year was used to control for inter-year variance, by including this covariate in all 17 candidate models except the null model. If information on any covariate was unavailable (10 nests lacking data on female age and condition), such cases were omitted from our analysis, resulting in 53 successful and seven deserted nests.

The binary response variable necessitates logistic regression models. Some females (13%, *N* = 7) were observed in both years, which violates the assumption of independence and would thus call for the use of a mixed-model nested design, with observations nested within the random factor 'female' to control for repeated sampling across error terms. However, we refrained from this approach, since the best analysis technique of logistic generalized linear mixed models is debated (Breslow & Lin 1995), and such techniques also complicate the application of AIC, thereby jeopardizing our aim of objectively selecting amongst candidate variables. Furthermore, our use of the two-level covariate year partly corrects for the few repeated observations of females.

The model selection and inference paradigm of Burnham and Anderson (2002) was applied to rank models for their ability to explain our data. The approach balances goodness of fit against the number of parameters, so that complex models are penalized. The models were ranked by using

Table 1. Covariates selected to explain the nest desertion patterns observed and their abbreviations divided into covariate classes.

Covariate class	Covariate	Abbreviation
Non-natal eggs	Number of non-natal eggs	NNE
Female characteristics	Own clutch size	OC
	Laydate	LAY
	Age	AGE
	Condition	COND
Environment	Temperature	TEMP
	Year	YR

AICc, a modified version of Akaike's information criterion, because N/P (sample size/number of parameters) was less than 40 (Burnham & Anderson 2002). We made inferences from the top-ranked model, the identity of which could be unambiguously defined if ΔAICc between the first and second ranked model was ≥ 2 (Burnham & Anderson 2002). In order to assess the independent and joint effects of the parameters in the top-ranked model, we employed hierarchical partitioning (HP) (Chevan & Sutherland 1991). The independent contribution of a predictor variable x is calculated by comparing the fit of all models including x with their reduced version (i.e. the same model with x omitted) within each hierarchical level. The average improvement in fit for each hierarchical level that considers x is then averaged across all hierarchies, giving the independent contribution of x (Quinn & Keough 2002). Joint effects are those caused by multicollinearity between predictors that restrict the explanatory power of the top-ranked model. The contribution of a predictor in conjunction with all others is found by subtracting the total variance explained by a predictor independently (as defined above) from the total variance explained by the predictor alone in a univariate model. Hence, HP allows identification of the predictors that explain most of the variance independent of the others, helping to overcome problems associated with multicollinearity. A parameter is highly collinear with the others if the joint effects exceed the independent effects. Parameters which dampen or act in opposition to the effect of others achieve negative values as their joint effect.

The information-theoretic approach taken here excludes the conventional use of p values for the determination of statistical significance; however, 95% confidence intervals (CI) are reported and can be used as an inference of significance. If the confidence interval does not include zero, the result can be regarded as 'significant'.

Results

Frequency of non-natal eggs

Among sampled nests, 57 out of 99 (58%) contained at least one non-natal egg, representing

21% ($N = 229$) of all sampled eggs ($N = 1098$). The mean (\pm SD) number of non-natal eggs in nests of recipients was 2.24 (± 2.6 , $N = 99$) for both years combined, the number of non-natal eggs ranging from 0 to 9 eggs. The years did not differ in the number of non-natal eggs in the nests of recipients, the mean difference ($\pm 95\%\text{CI}$) being 0.63 (± 1.03 , $N = 99$) eggs. Non-natal eggs represented on average (\pm SD) 16.6% (± 1.79) of the total eggs in the nests, ranging from 0% to 61.5%. The number of donor females laying eggs in recipient nests were on average (\pm SD) 1.43 (± 0.81) and ranged from one to five, the mode being one.

Factors affecting clutch desertion

The AICc ranking singled out one superior model which differed by $> 2\Delta\text{AICc}$ (Table 2) from the second ranked model. This model contained the number of non-natal eggs, own clutch size and year as predictors (Table 3). The probability of clutch desertion increased with both the number of non-natal eggs in the nest (Fig. 1) and the recipient's own clutch size, and it was higher in 2005 than in 2006 (Fig. 2). The following logistic regression formula of the top ranked model was used for inference, where NNE is the number of non-natal eggs in the nest, OC the number of natal eggs in the clutch, and YR is year.

$$P = \frac{\exp(-6988.2 + 0.40\text{NNE} + 0.70\text{OC} - 3.49\text{YR})}{1 + \exp(-6988.2 + 0.40\text{NNE} + 0.70\text{OC} - 3.49\text{YR})} \cdot (1)$$

Hierarchical partitioning

Hierarchical partitioning showed that the effects of the parameters were predominantly independent of each other, suggesting that multicollinearity did not bias our parameter estimates. Year, non-natal eggs and own clutch size all had strong independent effects (Fig. 3). The joint effects were small in comparison, non-natal eggs having the smallest and own clutch size the largest joint effect (Fig. 3). The negative values for joint effects of year and own clutch size show that these parameters when acting jointly suppress the effects of other parameters.

Table 2. AICc table of 17 models, each representing specific hypotheses describing the nest desertion pattern observed. Models are ranked by AICc values and the top ranking model differed from the second-ranked model by more than 2 units ($\Delta\text{AICc} > 2$) and was used for hierarchical partitioning of variance. Model rank, model composition, deviance ($-2\log$ likelihood), number of parameters, AICc value, ΔAICc , and AIC weight is showed for each model.

Rank	Model	Deviance	<i>P</i>	AICc	ΔAICc	AIC weight
1	YR + NNE + OC	24.72	4	33.44	0.00	0.66
2	YR + OC	29.83	3	36.26	2.82	0.16
3	YR +NNE+OC + LAY+COND+AGE	22.43	7	38.59	5.14	0.05
4	YR +NNE+TEMP+OC + LAY+COND+AGE	21.64	8	40.46	7.02	0.02
5	YR + NNE+LAY	31.78	4	40.51	7.06	0.02
6	YR + OC + LAY+COND+AGE	26.98	6	40.56	7.12	0.02
7	YR + NNE	34.20	3	40.62	7.18	0.02
8	YR + NNE+COND	32.01	4	40.74	7.29	0.02
9	YR + NNE +AGE	32.23	4	40.96	7.52	0.02
10	YR + AGE	36.06	3	42.49	9.05	< 0.01
11	YR + COND	36.35	3	42.78	9.33	< 0.01
12	YR + TEMP + OC + LAY + COND + AGE	26.84	7	42.99	9.55	< 0.00
13	YR	40.17	2	44.38	10.93	< 0.01
14	YR + NNE + TEMP	34.14	5	45.26	11.81	< 0.01
15	NULL	43.23	1	45.30	11.85	< 0.01
16	YR + TEMP	39.69	3	46.12	12.67	< 0.01
17	YR + LAY	40.16	3	46.59	13.14	< 0.01

Discussion

The presence of non-natal eggs, recipient’s own clutch size, and a year effect best predicted the probability of nest desertion. Nest parasitism was more common than previously reported for this species (Eadie & Fryxell 1992), and this behaviour profoundly affected the nesting suc-

Table 3. Parameter estimates for the parameters in the top-ranked AICc model.

Parameter	Value	SE	<i>z</i>	95%CI
Year	−3.49	1.74	2.00	3.49
Non-natal eggs	0.40	0.20	2.05	0.39
Own clutch size	0.70	0.28	2.5	0.56

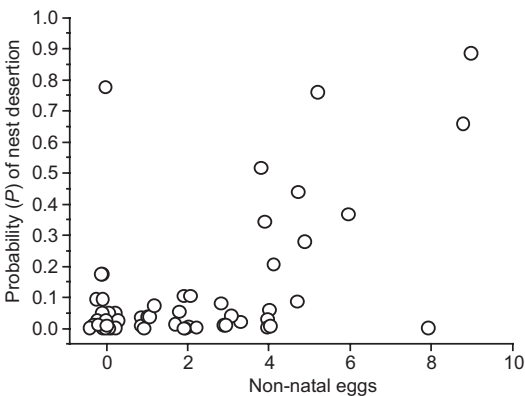


Fig. 1. The relationship between the probability of nest desertion and the number of non-natal eggs. Probabilities are calculated using Eq. 1. A random jitter with the mean = 0 and SD = 0.15 was added to the variable ‘non-natal eggs’, to visualize overlapping data points.

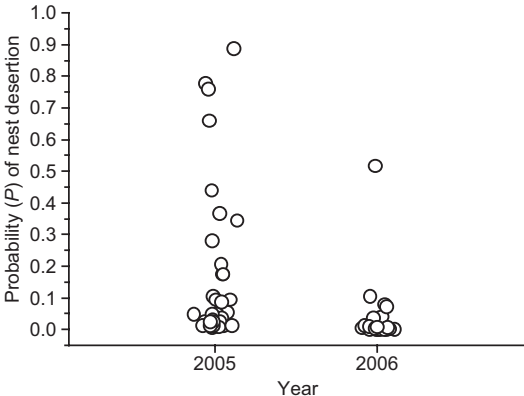


Fig. 2. The relationship between the probability of nest desertion and year. Probabilities are calculated using Eq. 1. A random jitter with the mean = 0 and SD = 0.05 was added to the variable ‘year’, to visualize overlapping data points.

cess of breeding females by elevating the probability of nest desertion. The probability of nest desertion also increased as the female's own clutch size increased (but *see* below), and it differed between the two years. This year effect may reflect differences in environmental conditions other than temperature, which was found to have no significant effect on the probability of nest desertion. There was also no demonstrable effect of host age on the probability of nest desertion; this lack of effect may be real or because the minimum age estimates used by us are imperfect metrics of female experience.

Our findings suggest that the behaviour of egg donors reduce the fitness of recipients, lowering their incentive to care for the current clutch. No clutches received additional eggs after the last observation of the female tending the nest, and thus the possibility of reversed causality underlying this finding — that is, that deserted nests are more likely to be parasitized, rather than parasitized nests being more likely to be deserted — can be excluded. The negative effect of non-natal eggs on the nesting success of egg recipients (*see* also Andersson & Eriksson 1982), after controlling for environmental factors and host-specific characteristics on nest desertion, is clear. While McRae (1995) also found an elevated risk of nest desertion due to parasitism in the semi-precocial moorhen (*Gallinula chloropus*), there are aspects of moorhen breeding biology that tend to moderate any negative effects of increased nest desertion. In contrast to the Barrow's goldeneye, female moorhens typically complete their clutch in a new nest immediately following nest desertion. Such mitigating circumstances are less likely in Barrow's goldeneyes, where alternative nest cavities may be hard to find.

Our result contradicts the view that addition of non-natal eggs inflicts only marginal costs on the recipient in precocial species (reviewed in Eadie *et al.* 1988). It has been suggested that extra offspring would only require unshared forms of parental investment (*sensu* Lazarus & Inglis 1986). If so, extra offspring would not represent a cost to the caring female (Ruusila & Pöysä 1998), allowing the egg donor strategy to persist in the population as selectively neutral to recipients. However, our results show that there are negative effects of egg addition

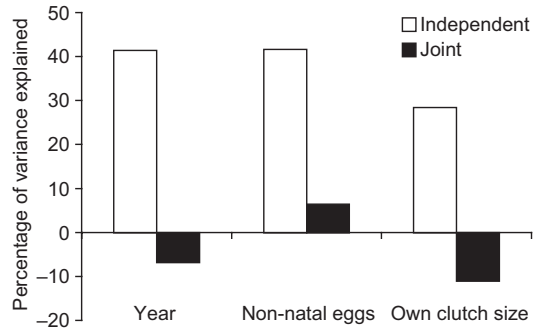


Fig. 3. Percentage of variance explained by the parameters in the top-ranked model independently and jointly with other parameters. The predominance of independent effects indicates low multicollinearity. Negative joint effects indicate that the parameter in question has a suppressing effect when acting in concert with other parameters.

on recipients already during the nesting stage, comparable with elevated incubation costs due to clutch enlargement found in altricial species, such as the great tit (*Parus major*) (de Heij *et al.* 2006). Our study focused only on nests in which incubation was initiated and 'dump nests', which were abandoned prior to the onset of incubation, were excluded, since female breeding intentions and host-parasite identities in such nests were unclear. However, desertion before incubation begins may well represent an additional means of avoiding the negative impacts of non-natal eggs in the nest. Elucidating host-parasite interactions prior to incubation onset would therefore provide interesting new avenues of research.

To fully understand the evolutionary dynamics of egg donors and recipients, the inclusive fitness achieved by both parties need to be considered. Receiving non-natal eggs may provide direct fitness benefits for the host, by elevating the survival of young through dilution of predation risk (Eadie *et al.* 1988, Whitfield 2003, Boland 2003), or indirect fitness benefits through rearing the offspring of close kin (Andersson 2001, Lopez-Sepulcre & Kokko 2002). Indeed, there are indications of positive effects of brood size on offspring survival in Barrow's goldeneyes (Smith *et al.* 2005), as well as in other precocial species such as white-winged scoters (*Melanitta fusca deglandi*) (Kehoe 1989), eiders (*Somateria mollissima*) (Öst *et al.* 2008) and geese (Lepage *et al.* 1998, Loonen *et al.*

1999). The outcome of nest parasitism is essentially clutch enlargement, which in turn results in brood enlargement. Thus, females who are able to overcome the cost of incubating a larger clutch may be able to enhance their fitness.

A larger own clutch size seemed to elevate the probability of nest abandonment, which contradicts the expectation that females should invest more in larger clutches with higher expected fitness returns (e.g. Williams 1966). However, we suspect that the relatively low variability of protein fingerprints in this study, resulting in a considerable risk of scoring non-natal eggs as host eggs, may at least partly explain this result. Thus, an examination of the range of own clutch sizes recorded in this study revealed that 10% of all clutches contained more than 12 eggs, exceeding the maximum clutch size for this species (Eadie 1989). This will lead to overestimation of the effect of own eggs and underestimation of that of non-natal eggs on the probability of nest desertion. Moreover, pointing to a link between own clutch size and later parental investment, increased own clutch size seemed to reduce the effect of others on nest desertion, a pattern sharply contrasting with the joint effect of non-natal eggs on the risk of nest desertion (Fig. 3). Whether a larger own clutch in itself increased the likelihood of desertion therefore remains an open question.

Another possibility, perhaps less likely, is a mismatch between own clutch size and the environment and/or the behaviour of egg donors, in which hosts unable to adjust their clutch size to the prevailing conditions may suffer lowered fitness. However, we found no significant reduction in hatchability of eggs (mean proportion of eggs hatched \pm SD = 0.91 ± 0.11) as a result of increased total clutch size (Pearson correlation: $r = -0.13$, $N = 53$, $p = 0.37$), but this analysis only included the female cohort successfully completing incubation. The female's decision to incubate or desert the clutch thus seems to be the main determinant of hatching success.

Life-history theory predicts stabilizing selection on clutch size owing to a trade-off between fitness benefits of a large clutch and costs of producing and incubating it (e.g. de Heij *et al.* 2006). If nest parasitism is frequent yet highly variable in occurrence, however, one would

expect phenotypic plasticity in egg production, to allow compensation when there are many non-natal eggs in the nests. Indeed reduced own clutch in response to experimental nest parasitism has been recorded in both common goldeneyes (Andersson & Eriksson 1982) and eiders (Erikstad & Bustnes 1994). We suggest controlled experiments in combination with the use of high resolution molecular markers to further clarify the importance of clutch size regulation in determining female nesting success.

Determining the occurrence and fitness effects of non-natal eggs for recipients is a crucial step in furthering our understanding of nest parasitism from the perspectives of both egg recipients and donors. For example, quantifying the costs and benefits of this behaviour can help clarify whether kin selection plays a role in maintaining it (e.g. Andersson & Åhlund 2000, Pöysä 2004, Roy-Nielsen *et al.* 2006, Andersson & Waldeck 2007, Waldeck *et al.* 2008). We found that receiving non-natal eggs has an unequivocal negative effect on the probability of nesting successfully; however, a recipient able to successfully complete incubation may obtain a net fitness benefit as regards offspring survival until fledging (Eadie *et al.* 1988, Smith *et al.* 2005). As a next step towards estimating the realized inclusive fitness benefits for both parties involved, we suggest determining the relatedness between egg recipients and donors.

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