Incubation capacity contributes to constraints on maximal clutch size in Brent Geese *Branta bernicla nigricans*

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Lack (1967) proposed that clutch size in species with precocial young was determined by nutrients available to females at the time of egg formation; since then others have suggested that regulation of clutch size in these species may be more complex. We tested whether incubation limitation contributes to ultimate constraints on maximal clutch size in Black Brent Geese (Black Brant) *Branta bernicla nigricans*. Specifically, we investigated the relationship between clutch size and duration of the nesting period (i.e. days between nest initiation and the first pipped egg) and the number of goslings leaving the nest. We used experimental clutch manipulations to assess these questions because they allowed us to create clutches that were larger than the typical maximum of five eggs in this species. We found that the per-capita probability of egg success (i.e. the probability an egg hatched and the gosling left the nest) declined from 0.81 for two-egg clutches to 0.50 for seven-egg clutches. As a result of declining egg success, clutches containing more than five eggs produced, at best, only marginally more offspring. Manipulating clutch size at the beginning of incubation had no effect on the duration of the nesting period, but the nesting period increased with the number of eggs a female laid naturally prior to manipulation, from 25.4 days (95% CI 25.1–25.7) for three-egg clutches to 27.7 days (95% CI 27.3–28.1) for six-egg clutches. This delay in hatching may result in reduced gosling growth rates due to declining forage quality during the brood rearing period. Our results suggest that the strong right truncation of Brent clutches, which results in few clutches greater than five, is partially explained by the declining incubation capacity of females as clutch size increases and a delay in hatching with each additional egg laid. As a result, females laying clutches with more than five eggs would typically gain little fitness benefit above that associated with a five-egg clutch.

Keywords: *Branta bernicla nigricans*, egg survival, hatchability, incubation limitation hypothesis, life-history trade-offs, nesting period, optimal clutch size.

David Lack pioneered ideas about regulation of clutch size in birds (Lack 1947). Lack proposed that in birds with altricial young, optimal clutch size is determined by the maximal number of offspring that parents can feed until fledging (Lack 1947, 1954). Alternatively, because species with precocial young do not feed their offspring, Lack hypothesized that clutch size in waterfowl (family Anatidae) was entirely determined by the nutrients available to the female during egg-laying (Lack 1967). He based this hypothesis, which is often labelled the 'egg production hypothesis' (EPH), on the observation that across taxa in the Anatidae there is a negative correlation between clutch size and egg size, suggesting a trade-off regulated by nutrients (Lack 1967).

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Since Lack's work, some studies have found support for the EPH by correlating pre-laying nutrient reserves with clutch size (Ankney & Macinnes 1978, Drent & Daan 1980, Sedinger *et al.* 1997). Others have pointed to high variation in post-laying nutrient reserves among females (Arnold & Rohwer 1991), and strongly right-truncated clutch size distributions (Winkler & Walters 1983), as indications that the EPH alone may not entirely explain variation in clutch size in species with precocial young. As a result, several researchers have suggested that rigorous tests of alternative or additional mechanisms of clutch size regulation in precocial species are warranted (Arnold *et al.* 1987, Arnold & Rohwer 1991, Rohwer 1992, Williams 2012).

Tests of Lack's hypothesis that have relied on brood size manipulations have often found that parents can successfully fledge more offspring than were produced by their clutch (Vander Werf 1992, Sedinger *et al.* 2017). This paradox motivated work to test for trade-offs between brood size, residual reproductive value of parents and offspring quality and recruitment rate, which could contribute to clutch size regulation (Stearns 1992). However, as Monaghan and Nager (1997) pointed out, many studies testing for trade-offs ignored the fact that phases other than brood rearing, for example the incubation period, could also contribute to clutch size regulation. For instance, the 'incubation limitation hypothesis' predicts that as clutch size increases, the attending parent or parents are unable to successfully

incubate additional eggs, which eventually results in no additional offspring being produced and a prolonged nesting duration, resulting in increased predation risk (Lack 1947, Arnold 1999). In some species, such as Arctic nesting geese, delayed hatching of the clutch may also create a mismatch between the hatching of offspring and the quantity or quality of their forage, resulting in reduced growth rates and lower lifetime fitness (Cooch *et al.* 1991, Sedinger & Flint 1991, Sedinger *et al.* 1995, Sedinger & Chelgren 2007).

Although some researchers have questioned the role of the incubation limitation hypothesis in regulating clutch size in birds with precocial young (e.g. Rohwer 1985, Sandercock 1997), Arnold (1999) argued that some of the apparent lack of support for the incubation limitation hypothesis has resulted from researchers not simultaneously assessing all components of fitness during nesting to estimate the total reproductive value of the clutch. The possibility that incubation ability could contribute to clutch size regulation in waterfowl has rarely been experimentally tested (but see Rohwer 1985).

Our goal in this paper was to test the incubation limitation hypothesis in Brent Geese (Black Brant) *Branta bernicla nigricans*. Our objective was not to falsify the EPH in Brent Geese, but to understand whether there is potential for incubation limitation to contribute to an explanation for the strong truncation of clutches with more than five eggs (Fig. 1a) in this species. We used experimental manipulations of clutch size because this
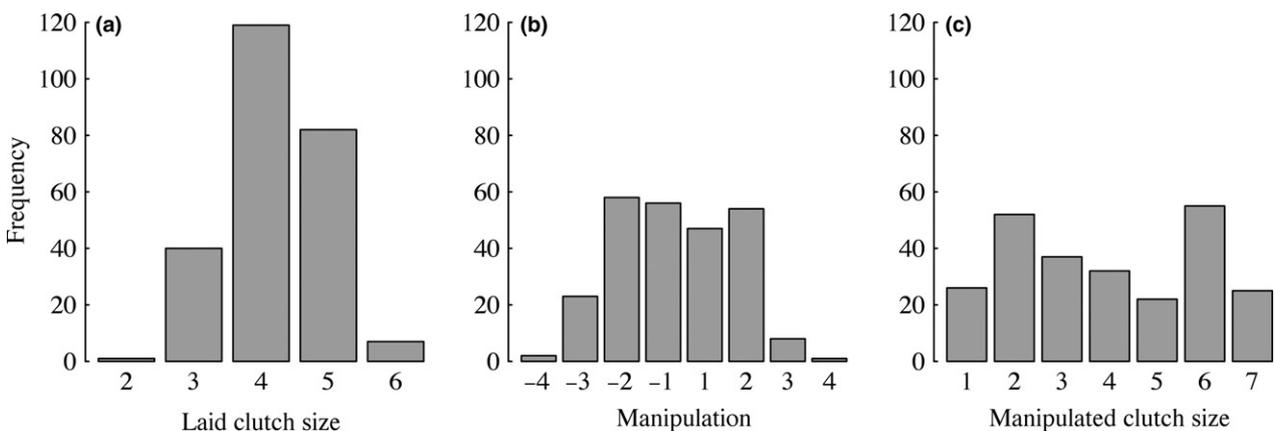

Figure 1. (a) Number of clutches, ranging from two to six eggs, laid by Brent Goose females, (b) relative experimental manipulation of clutch size by investigators, and (c) final clutch sizes created after manipulations at the Tutakoke River colony, Alaska, USA, from 2008 to 2012.

enabled us to create clutches with more than five eggs to assess whether maximal clutch size in Brent might be constrained by incubation capacity. Additionally, clutch size manipulations reduce the relationship between parental quality and reproductive output, which are typically positively correlated (van Noordwijk & de Jong 1986). In our case, we were concerned with a potentially positive relationship between the clutch size laid by the female and her ability successfully to incubate additional eggs.

We predicted that if incubation limitation contributes to maximal clutch size constraints in Brent, experimental clutches larger than the common natural maximum (five eggs) would not, on average, produce more goslings and would take longer to hatch. To test these predictions, we estimated the effects of clutch size on the probability of eggs surviving to hatch, the probability of egg success (i.e. probability an egg hatched and the gosling left the nest), the duration of the nesting period (i.e. time in days from nest initiation to first pipped egg) and the average number of goslings produced by each clutch size. Additionally, we wanted to assess whether females laying clutches smaller than five did so because these clutches maximized the number of goslings in their initial brood (i.e. the individual optimization hypothesis; Hogstedt 1980, Pettifor *et al.* 1988, 2001). To test the individual optimization hypothesis, we compared the number of goslings produced from reduced and enlarged clutches with non-manipulated clutches. We predicted that if a female optimized her clutch size to produce the maximal number of goslings, experimental reduction or enlargement of clutch size would result in fewer offspring leaving the nest.

METHODS

Study site and species

We conducted our study from 2008 to 2012 at the Tutakoke River Brent Goose colony (61°15′N, 165°37′W) on the Yukon-Kuskokwim Delta in southwestern Alaska, USA. The Tutakoke River study area is approximately 5 km^2 in size and located adjacent to the Bering Sea. During the years of our study, the number of Brent Goose nests at Tutakoke River ranged from approximately 600 to 3300 (Wilson 2014). Brent Geese nest in wet sedge *Carex ramenskii* meadows and

on islands of vegetation surrounded by intertidal mudflats; nests are occasionally inundated during high tide events (Lindberg & Sedinger 1997). Brent Geese form perennial, socially monogamous pair-bonds, with partners remaining in close contact throughout the annual cycle (Bellrose 1980, Leach 2015). Brent Goose females are determinate layers and assume all incubation duties during the nesting period (Eichholz & Sedinger 1998). Within about 48 h of hatch, Brent Goose goslings are mobile and disperse with parents to sedge *Carex subspathacea* grazing lawns (Flint *et al.* 1995, Sedinger *et al.* 2001).

Nest monitoring

As soon as egg-laying began each season (mid-May), we searched for newly initiated Brent Goose nests (i.e. with one or two eggs and a small amount of down). When a nest was located, we determined its initiation date and recorded the number of eggs present. We considered nests found with one egg to have been initiated that day and those found with two eggs to have been initiated the day before. We excluded nests found with more than two eggs because assigning an initiation date to such nests was not sufficiently accurate for the current analysis. We assigned a unique nest number, and mapped the location of each nest on an aerial photograph. We used a permanent marker to write the nest number and position in the laying sequence on each egg. If a nest contained more than one new egg at a subsequent visit, we used staining to determine laying sequence (Flint & Sedinger 1992). We monitored marked nests daily during egg-laying, and once a clutch was complete (i.e. no new eggs for 48 h) it was eligible for experimental manipulation. During incubation, we checked nests two to three times and recorded any predation, flooding or abandonment of eggs. Once hatching began, we checked manipulated nests daily to determine whether each egg was successful, and the number of goslings leaving the nest. We calculated the number of goslings leaving the nest by subtracting the number of predated eggs, unhatched eggs and goslings that died in the nest from the total post-manipulation clutch size (see below).

Clutch manipulations

To maintain hatching synchrony among eggs in a nest, we only moved eggs between clutches with

the same number of eggs and initiation date (Nicolai *et al.* 2004). We attempted to create a relatively uniform range of experimentally manipulated clutch sizes; therefore, not all females were subjected to equal treatments (Fig. 1b). For instance, the maximal final clutch size we created was seven eggs, so the maximal relative clutch enlargement possible for females that laid five eggs was smaller (i.e. two eggs) than that for females that laid three-egg clutches (i.e. four eggs). Thus, the treatments applied to individual nests were random with respect to our desired goal of creating final clutch sizes ranging from one to seven eggs (Fig. 1c) but not equal in magnitude by laid clutch size (Table 1). Our manipulations of individual clutches ranged from removing four eggs to adding four eggs (Fig. 1b).

Clutch manipulations were performed within 72 h of clutch completion. We carried eggs in insulated bags between nests that were typically < 75 m apart; moved eggs were out of a nest for less than 5 min. Nests were subsequently checked two to three times during incubation to monitor egg fate. At hatching, we recorded whether each egg hatched (i.e. star-pipped) and given hatching, whether or not the gosling left the nest. We did not include nests that also received a brood manipulation during hatching as part of another study (Sedinger *et al.* 2017). During our study, we experimentally manipulated 337 clutches. Of these, we excluded 56 nests (16.7% of sample) that were destroyed by inundation during high tide events, because we reasoned that flooding was random with respect to manipulated clutch size, and inclusion of these nests would have added unnecessary variability. We documented 32 nests that were abandoned after manipulation. Percentages of

manipulated clutches abandoned were: 7.1% (one egg), 1.9% (two eggs), 2.6% (three eggs), 5.9% (four eggs), 12% (five eggs), 19.1% (six eggs) and 28.6% (seven eggs). Of the 32 nest abandonments, two occurred during the hatching period, while all other abandonments were during incubation. We removed abandoned clutches from our analysis (Sandercock 1997, Arnold 1999). However, to demonstrate that our conclusions would be similar with abandonments included, we modelled the number of goslings leaving the nest with and without abandoned nests. Our final dataset, excluding nest abandonments, included 984 eggs from 249 experimentally manipulated clutches (Table 1). Our manipulations reduced, but did not eliminate ($r = 0.33$, $P < 0.001$), the correlation between laid clutch size and final clutch.

From our full dataset of clutch manipulations, which included some nests that underwent brood manipulations after their hatching date was recorded, we determined the nesting duration of 243 nests. In this analysis, we only included clutches that hatched at least one egg. We calculated the duration of nesting as the time (in days) between when the first egg was laid and when the first egg pipped. We recorded an egg as pipped when the first evidence of shell fracturing by the gosling appeared (i.e. star-pipped). We recognize that researchers may use different metrics to estimate hatching date (e.g. nestling leaving the egg); however, our methodology was similar to previous work on this population (Eichholz & Sedinger 1998) and consistently recorded among nests.

Statistical analyses

Given the small number of explanatory variables considered in each analysis, we only considered a full model containing the variables described for each analysis (see below). We did not perform any model selection and report all parameter estimates from the saturated model for each analysis.

To examine potential variation in hatching success (i.e. the probability a gosling star-pipped the eggshell) and egg success (i.e. the probability an egg hatched and the gosling left the nest), we built generalized linear mixed-models (binomial distribution with logit link) using the *glmer* function in program R 2.10.0 (R Core Team 2014). To account for a potential lack of independence among eggs incubated in the same nest, we included a random intercept for incubation nest,

Table 1. Numbers of final manipulated clutch sizes by laid (natural) clutch size at the Tutakoke River Brent Goose colony, Alaska, USA, 2008–2012.

Laid clutch	Final clutch							Total
	1	2	3	4	5	6	7	
2	0	0	1	0	0	0	0	1
3	9	13	0	10	5	2	1	40
4	15	32	18	0	14	34	6	119
5	2	7	17	22	0	19	15	82
6	0	0	1	0	3	0	3	7
Total	26	52	37	32	22	55	25	

inclusion of which reduced the Akaike Information Criterion adjusted for small sample size (AICc) of models for hatching and egg success by > AICc 137 units. A correlation in hatching success of eggs laid by the same female may exist, irrespective of the nest they are incubated in; however, inclusion of an additional random intercept for genetic female improved model fit by < 2.4 AICc units, probably because any genetic correlation was small compared with variation in the nesting environment among female. Thus, we did not include a random effect for genetic females. To model variation in hatching and egg success as a function of manipulated clutch size, we created a categorical variable, MCS, which ranged from one to seven eggs (Fig. 1c) because our main objective was to compare reproductive success of all other final clutch sizes with those containing five eggs (i.e. the largest common clutch size laid by Brent Geese); we used five-egg clutches for the reference level of MCS in all analyses. We used the categorical variable YEAR (2008–2012) to account for variation in nest survival and partial predation rates among years not related to our variables of interest. To test for the potential that moving an egg to a host nest reduced its success, we created the covariate MOVED. We used the continuous covariate CS to measure the effect of laid clutch size on incubation ability. To produce estimates of hatching and egg success as a function of MCS on the probability scale we used 1000 parametric bootstrap simulations, which incorporated the random variation among nests and our fixed effects (Fig. 2a,b).

To estimate the average number of goslings leaving the nest (GLN) from each manipulated clutch size (MCS), we built a generalized linear model (Poisson error distribution) using the *glm* function in program R 2.10.0 (R Core Team 2014). To model variation in GLN we included the categorical variables YEAR and MCS and a continuous covariate for laid clutch size (CS).

To test for individual optimization of clutch size, we only considered clutches where the female laid three, four or five eggs because they provided adequate sample sizes and are the clutches typically laid by Brent Geese (Fig. 1a). We only included manipulated clutches with relative manipulations from −2 to +2 eggs for this analysis, because they represented much of our sample (84%) and all laid clutches were manipulated within this range (Table 1). As a control group, we included three-egg (n = 432), four-egg (n = 731) and five-egg
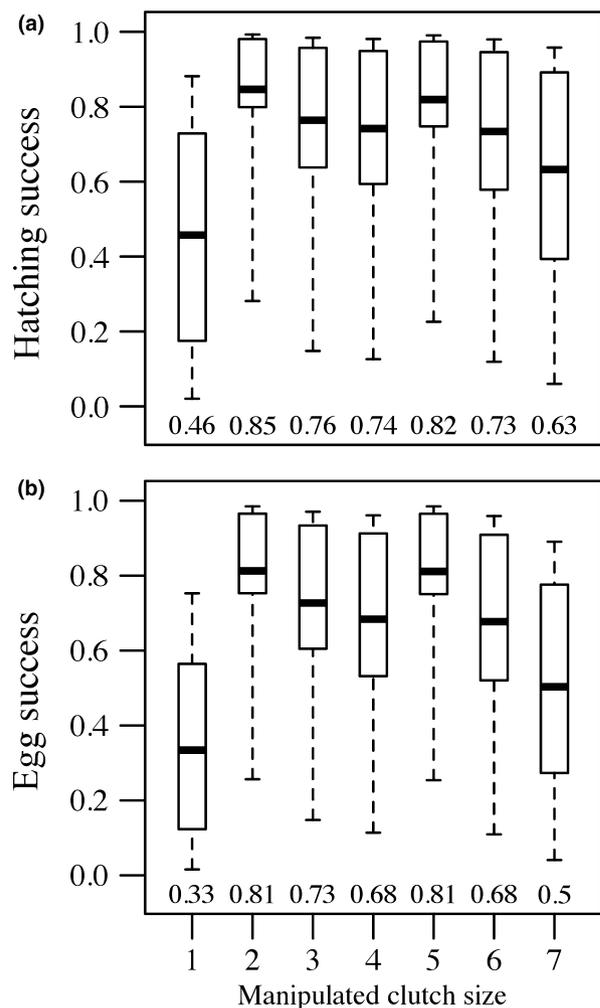

Figure 2. (a) Hatching success (see Table 2 caption) and (b) egg success (see Table 3 caption) as a function of manipulated clutch size of adult female Brent Geese at Tutakoke River colony, southwestern Alaska, USA, from 2008 to 2012. Means are indicated below each error bar. Line indicates mean probability of success, box the upper and lower quartiles, and whiskers 2.5 and 97.5 percentiles.

clutches (n = 530) that were not manipulated but were laid in the same years as clutches that were manipulated. We combined clutch reductions, controls and enlargements into three respective categories. Our response variable in this analysis was the number of goslings leaving the nest. We built a generalized linear model (Poisson error distribution) and included YEAR and an interaction between laid clutch (categorical variable) and manipulation category in this analysis.

To examine potential variation in the duration of nesting, we built a generalized linear model

(Gaussian error distribution) using the *glm* function in program R 2.10.0 (R Core Team 2014). In addition to the variables YEAR and MCS, we used the continuous covariate CS, because the number of eggs laid by the female has been shown to affect nesting duration in Brent Geese (Eichholz & Sedinger 1998).

RESULTS

Hatching and egg success

When compared with clutches containing five eggs at the end of laying, eggs in clutches with seven eggs were less likely to hatch (Table 2, Fig. 2a). In general, hatching success increased sharply from one- to two-egg clutches, and then declined as manipulated clutch size increased (Fig. 2a). The parameter estimate for the variable MOVED indicated that being moved to a host nest explained little or no variation in the probability that an egg hatched (Table 2).

For our analysis of the probability that an egg successfully transitioned to a gosling that left the nest, based on the number of eggs incubated, our results indicated that when compared with clutches containing five eggs after experimental manipulation, eggs in seven-egg clutches had a lower probability of being successful (Table 3, Fig. 2b). Laid clutch size was positively related with egg success (Table 3). The parameter estimate for the variable MOVED indicated that being moved to a host nest explained little variation in the probability an egg successfully transitioned to a gosling (Table 3).

Number of goslings leaving the nest

Manipulated clutches containing four or fewer eggs at the end of laying all produced fewer goslings than did five-egg clutches (Table 4, Fig. 3a). Estimates of GLN for six- and seven-egg clutches were not significantly greater than for manipulated clutches containing five eggs (Table 4, Fig. 3a),

Table 2. Coefficient estimates ($\hat{\beta}$, logit scale), standard errors (se) and *P*-values for the generalized linear mixed effect model (binomial error distribution) examining variation in hatching success (i.e. the probability a gosling star-pipped the eggshell) of Brent Goose eggs in experimentally manipulated nests at the Tutakoke River colony, Alaska, USA, from 2008 to 2012. The categorical variables included in the model are study year, whether an egg was transferred to a host nest for incubation (MOVED) and final manipulated clutch size (MCS), which varied from one to seven eggs. Laid clutch size (CS) represented the number of eggs the attending female laid prior to manipulation and was modelled as a continuous covariate. The intercept represents the logit of hatching success of eggs in clutches containing five eggs after manipulation, in 2009. The model included a random intercept for the nest an egg was incubated in, which had an estimated standard deviation of 2.166.

Parameter	$\hat{\beta}$	se	P
Intercept	0.78	1.24	0.530
YEAR (2008)	0.98	0.98	0.319
YEAR (2010)	−1.39	0.49	0.005
YEAR (2011)	−0.49	0.52	0.350
YEAR (2012)	0.98	0.57	0.087
CS	0.44	0.26	0.087
MOVED	−0.06	0.26	0.816
MCS (1)	−2.64	0.90	0.003
MCS (2)	0.29	0.70	0.673
MCS (3)	−0.52	0.73	0.476
MCS (4)	−0.71	0.76	0.351
MCS (6)	−0.77	0.66	0.244
MCS (7)	−1.52	0.78	0.051

Table 3. Coefficient estimates ($\hat{\beta}$, logit scale), standard errors (se) and *P*-values for the generalized linear mixed-model (binomial error distribution) examining variation in the success (i.e. the probability an egg hatched and the gosling left the nest) of Brent Goose eggs in experimentally manipulated nests at the Tutakoke River colony, Alaska, USA, from 2008 to 2012. The categorical variables included in the model are study year, whether an egg was transferred to a host nest for incubation (MOVED) and final manipulated clutch size (MCS), which varied from one to seven eggs. Laid clutch size (CS) represented the number of eggs the attending female laid prior to manipulation and was modelled as a continuous covariate. The intercept represents the logit of egg success of eggs in clutches containing five eggs after manipulation, in 2009. The model included a random intercept for the nest an egg was incubated in, which had an estimated standard deviation of 1.894.

Parameter	$\hat{\beta}$	se	P
Intercept	0.09	1.09	0.931
YEAR (2008)	−0.27	0.84	0.743
YEAR (2010)	−0.96	0.43	0.026
YEAR (2011)	−0.23	0.46	0.617
YEAR (2012)	0.38	0.49	0.438
CS	0.53	0.23	0.024
MOVED	0.01	0.24	0.959
MCS (1)	−3.06	0.82	< 0.001
MCS (2)	0.01	0.62	0.983
MCS (3)	−0.68	0.65	0.298
MCS (4)	−0.97	0.66	0.139
MCS (6)	−1.02	0.58	0.081
MCS (7)	−2.08	0.70	0.003

Table 4. Coefficient estimates ($\hat{\beta}$, logarithmic scale), standard errors (se) and *P*-values for the generalized linear model (Poisson error distribution) examining variation in the number of Brent Goose goslings that left the nest based on number of eggs in the nest after experimental manipulation at the Tutakoke River colony, Alaska, USA, from 2008 to 2012. The categorical variables included in the model are study year and final manipulated clutch size (MCS) which varied from one to seven eggs. Laid clutch size (CS) represented the number of eggs the attending female laid prior to manipulation and was modelled as a continuous covariate. The intercept represents nests with clutches containing five eggs after manipulation, in 2009.

Parameter	$\hat{\beta}$	se	P
Intercept	1.14	0.28	< 0.001
YEAR (2008)	−0.07	0.22	0.744
YEAR (2010)	−0.15	0.12	0.203
YEAR (2011)	0.06	0.11	0.607
YEAR (2012)	0.20	0.11	0.073
CS	0.05	0.06	0.414
MCS (1)	−2.59	0.39	< 0.001
MCS (2)	−0.90	0.16	< 0.001
MCS (3)	−0.60	0.16	< 0.001
MCS (4)	−0.37	0.16	0.025
MCS (6)	0.02	0.13	0.850
MCS (7)	0.01	0.16	0.990

indicating there was no support for the hypothesis that clutches greater than five produced more goslings. For manipulated clutches, laid clutch size did not affect the number of goslings that left the nest. Similarly, when we performed the analysis with abandoned nests included, we found that manipulated clutches with five eggs still produced the most goslings (Fig. 3b).

In our analysis testing the individual optimization hypothesis, we found that for three-egg clutches, adding eggs increased initial brood size from 2.19 (95% CI 2.00–2.38) in controls to 4.03 (95% CI 2.87–5.19) goslings for enlarged clutches (Fig. 4). Similarly, for four-egg clutches, adding eggs increased initial brood size from 3.33 (95% CI 3.12–3.53) for controls to 4.32 (95% CI 3.66–4.98) goslings for enlarged clutches. For females that laid five eggs, initial broods from control clutches contained, on average, 4.22 (95% CI 3.97–4.46) goslings and enlarged clutches produced 4.55 (95% CI 3.98–5.33) goslings, although the 95% confidence intervals for these estimates greatly overlapped, indicating little support for the prediction that adding eggs to five-egg clutches increased brood size (Fig. 4).

Duration of nesting

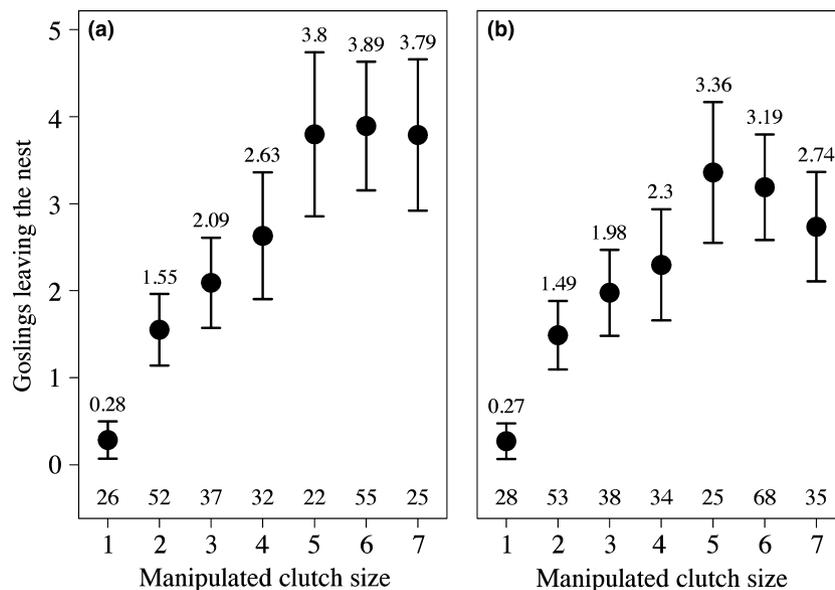None of the parameter estimates for the variable MCS differed from the reference category of five

Figure 3. Mean number of goslings produced by clutches containing one to seven eggs after experimental manipulation at the Tutakoke River colony, in southwestern Alaska, USA, from 2008 to 2012. Error bars represent 95% confidence intervals. Mean number of goslings reported above and number of manipulated clutches reported below the error bars. Panel (a) excludes nest abandonments and (b) includes nests which were abandoned.
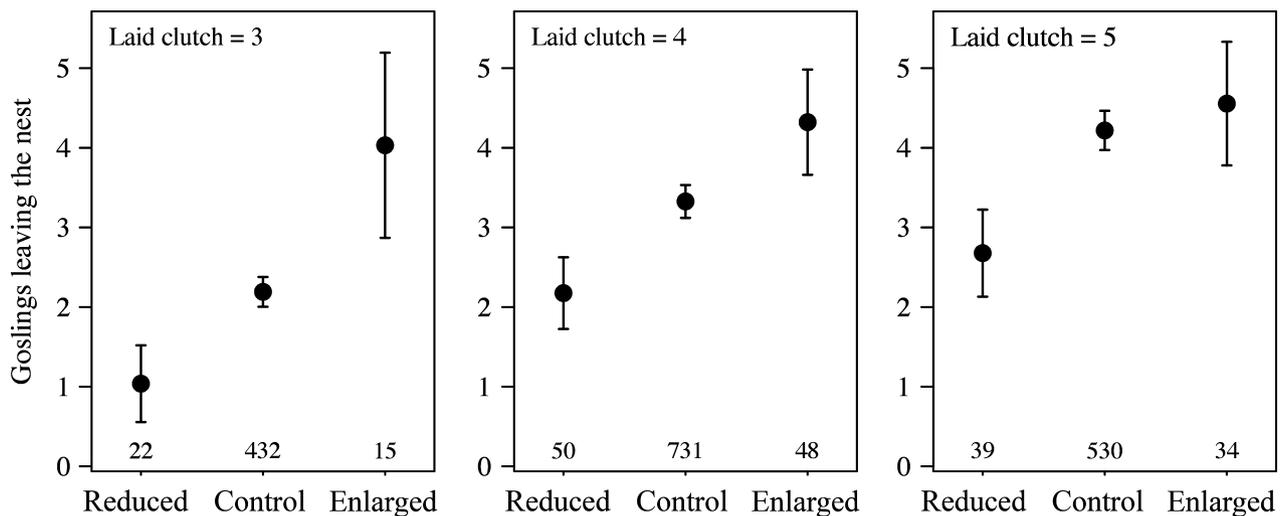
Figure 4. Mean number of goslings produced by experimentally reduced (−1 to −2 eggs), control (non-manipulated) and experimentally enlarged (+1 to +2 eggs) clutches at the Tutakoke River Brent Goose colony, southwestern Alaska, USA, from 2008 to 2012. Error bars represent 95% confidence intervals; number of clutches reported below error bars.

eggs, so we conclude that the number of eggs in the nest after laying is complete does not substantially alter the time needed to hatch a clutch (Table 5). However, the duration of nesting increased for each egg a female laid (Table 5, Fig. 5). As a result, nesting duration ranged from 25.4 days (95% CI 25.1–25.7) for clutches where three eggs were laid prior to manipulation to 27.7 days (95% CI 27.3–28.1) for six-egg clutches (Fig. 5).

DISCUSSION

We believe that our study provides evidence that incubation limitation provides a partial explanation for the rarity of Brent Goose clutches with more than five eggs. We base this on the result that manipulated clutches containing six or seven eggs produce, at best, only a marginal increase in the number of offspring that leave the nest compared to five-egg clutches (Table 4, Fig. 3). When eggs were added to clutches originally containing three or four eggs, females were clearly able to produce larger broods, indicating that the number of eggs they laid was not constrained by incubation ability. However, females that laid five-egg clutches, the largest common clutch, failed to produce considerably larger broods when clutches were enlarged, despite the fact that we found evidence that females laying five-egg clutches were able to

achieve higher egg success (Table 3). Thus, because of the residual correlation between natural and manipulated clutch size our results are conservative, whereby females with the greatest ability were more often given clutches greater than five and they were typically still unable to produce more goslings. These results indicate that incubation constraints in Brent Geese seem to contribute to a population-level upper limit on clutch size, with clutches greater than five, on average, producing virtually no additional offspring.

Our results demonstrate substantial variation in per-capita egg success as a function of the number of eggs incubated by female Brent Geese. The general pattern was that egg success increased sharply from one- to two-egg clutches and then declined with increasing clutch size thereafter (Fig. 2a,b). We suspect that single eggs had the lowest per-capita probability of becoming a gosling because these clutches could not sustain partial predation without being completely destroyed (Rockwell *et al.* 1987). Although, we cannot completely rule out the possibility that parental investment was reduced for one-egg clutches (Ackerman *et al.* 2003), resulting in increased predation risk or reduced egg viability. However, abandonment rates for one-egg clutches were relatively low (7.1%), suggesting that females were willing to tend these clutches. We believe that the per-capita decline in the probability of an egg becoming a

Table 5. Coefficient estimates ($\hat{\beta}$), standard errors (se) and *P*-values from a generalized linear model (Gaussian error distribution) examining variation in the duration of incubation (days from nest initiation to first pipping activity) of Brent Goose nests at the Tutakoke River colony, Alaska, USA, from 2008 to 2012. The categorical variables are study year and final manipulated clutch size (MCS). Laid clutch size (CS) represented the number of eggs the attending female laid prior to manipulation and was modelled as a continuous covariate. The intercept represents the duration of incubation of clutches containing five eggs after manipulation, in 2009.

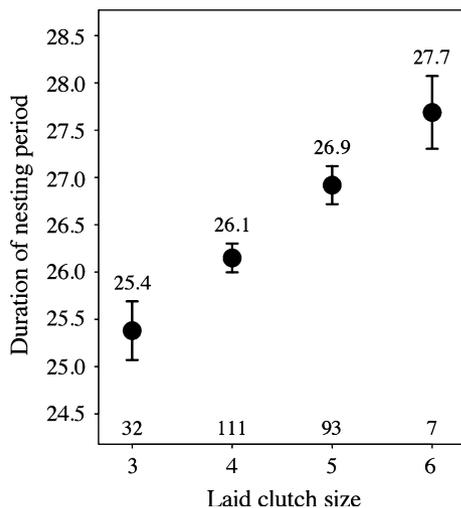| Parameter	$\hat{\beta}$	se	P
Intercept	23.12	0.50	< 0.001
YEAR (2008)	−0.68	0.38	0.075
YEAR (2010)	0.24	0.21	0.243
YEAR (2011)	−0.41	0.19	0.037
YEAR (2012)	−0.36	0.22	0.094
CS	0.77	0.11	< 0.001
MCS (1)	−0.04	0.40	0.918
MCS (2)	−0.07	0.27	0.789
MCS (3)	0.35	0.29	0.236
MCS (4)	−0.34	0.31	0.283
MCS (6)	0.28	0.26	0.297
MCS (7)	0.38	0.31	0.230

Figure 5. Predicted length of the nesting period as a function of laid clutch size for Brent Goose nests at the Tutakoke River colony, southwestern Alaska, USA, from 2008 to 2012. Means are indicated above and number of naturally laid clutches are reported below error bars. Error bars represent 95% confidence intervals.

gosling for clutches containing more than two eggs clearly indicates that female Brent Geese have a declining ability to successfully tend to each egg as clutch size increases.

Although our goal was to estimate the number of offspring produced from a range of clutch sizes rather than the exact mechanisms underlying such variation (e.g. egg viability vs. predation), we can deduce from our results that the declining reproductive value of larger clutches was largely caused by reductions in the probability that an egg hatched (Fig. 2a). However, we also found that an important component of egg success is the probability a gosling leaves the nest. We interpret the value of 1 − the quotient of egg success and hatching success (i.e. 1 − (egg success/hatching success)) as the proportion of egg failures that resulted from a gosling failing to leave the nest. Our results show that the proportion of egg failures resulting from goslings that do not leave the nest increases from two-egg (4.7%) to seven-egg clutches (20.6%). Thus, the declining probability that an egg became a gosling that left the nest as clutch size increased was caused by both declining hatching success and an increasing proportion of goslings failing to leave the nest.

We believe that manipulating clutch size improved our inferences about incubation capacity in Brent Geese for two reasons. First, we increased our sample size of clutches greater than five, adding power to our analysis (Fig. 1c). Secondly, a factor confounding the analysis of natural clutches in Brent is that a large proportion of clutches larger than six contain a parasitic egg that may not hatch synchronously with the eggs of the host female (Lemons *et al.* 2015) and could bias inferences about incubation capacity, a situation similar to that in Lesser Snow Geese *Anser caerulescens* (Rockwell *et al.* 1987). The fact that eggs we moved to a host nest were as successful as those remaining in their original nest suggests that we were able to match the hatching synchrony of moved and host eggs during the field experiment. Thus, because our manipulations maintained synchrony among eggs in large clutches, our study may have produced a less biased test of incubation capacity than if we had used natural clutches.

We acknowledge, however, that our artificial increases of clutch size may not have accounted for additional developmental asynchrony that could occur if female Brent Geese had laid the extra eggs (Arnold 1999). Thus, our results may be conservative concerning the decline in egg survival with increasing clutch size, because we could not simulate the potential asynchrony in hatch resulting from the laying interval between eggs,

30 h in the case of Brent Geese (J.S. Sedinger unpubl. data).

Rates of nest abandonment were greatest among the largest manipulated clutches, particularly those greater than normally laid by Brent Geese (five eggs). This result contrasts with several duck species (*Anas* spp.) that tended to increase abandonment after partial clutch loss due to predation (Ackerman *et al.* 2003). In our study, clutches that were experimentally reduced to contain one or two eggs had lower abandonment rates (1.9–7.1%) than those enlarged to contain six or seven eggs (19.1–28.6%). Thus, Brent Goose females may perceive these unnaturally large clutches as having a lower fitness value than those within the natural range. However, we agree with Arnold (1999) that the reason for abandonment is typically difficult to interpret. Inclusion of these abandoned nests had a disproportionately negative effect on the reproductive value of six- and seven-egg clutches but did not change the fact that, on average, five-egg clutches produced the largest initial brood sizes (Fig. 3b).

We found that hatching was delayed by 0.77 days for each egg a female laid. As a result, females that laid three eggs hatched their clutch about 2.3 days sooner than those laying six eggs. This delay in hatching date of larger clutches would negatively affect their fitness value by increasing their exposure to predation (Arnold *et al.* 1987) and reducing the growth rates of goslings (Sedinger & Flint 1991). A 2.3-day delay in hatch would result in goslings that weigh about 35.5 g less than their earlier hatching conspecifics at 30 days of age (Sedinger & Flint 1991). This reduction in growth during early life is not fully compensated for after fledging, and would result in a reduction in first-year survival, breeding probability and ultimately lower lifetime fitness for these smaller goslings (Sedinger *et al.* 1995, Sedinger & Chelgren 2007).

Manipulating the number of eggs in the nest after clutch completion had little effect on the duration of nesting. The exact mechanism underlying this increase in nesting duration with laid clutch size is unclear, but our results suggest that the variation results from events during laying and not from the number of eggs in the nest during incubation. A previous study on this population (Flint *et al.* 1994) showed that incubation in Brent Geese starts on the second egg; however, the dataset used in that paper only included four-egg clutches. Perhaps, the effect of laid clutch size on duration of nesting results from females beginning incubation relatively later in the laying sequence as clutch size increases.

In conclusion, our results suggest that the declining ability of female Brent Geese to successfully incubate eggs as clutch size increases results, at best, in a marginal increase in the number of offspring produced by clutches larger than five. Thus, we believe that our results provide a partial explanation for the strong right truncation of clutches larger than five in Brent. However, we do not suggest that our results completely explain variation in clutch size in Brent. For example, our results do not provide an explanation for why the most common clutch size is four eggs, because five-egg clutches, on average, produce more goslings (Fig. 3). We suspect that for clutches containing fewer than five eggs, nutrient limitation as proposed by Lack (1967) may play a role in clutch size determination. This paper is part of a series which aims to understand the effects of clutch size decisions on all fitness components of Brent Geese, so we do not draw our final conclusions about regulation of clutch size in Brent Geese from the current analyses. While we believe that the current analyses demonstrate that incubation limitation contributes to the reduced fitness value of clutches greater than five, and their rarity, in a future paper we hope to integrate all components of fitness, including the residual reproductive value of adult females, to understand more fully the suite of trade-offs that contribute to clutch size regulation in Brent Geese.

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