

Kittiwakes strategically reduce investment in replacement clutches

Julien Gasparini^{1,*}, Alexandre Roulin¹, Verena A. Gill^{2,3}, Scott A. Hatch²
and Thierry Boulinier⁴

¹Département d'Ecologie & Evolution, Université de Lausanne, 1015 Lausanne, Switzerland

²US Geological Survey, Alaska Science Center, 1011 East Tudor Road, Alaska 99503, USA

³US Fish and Wildlife Service, 1011 East Tudor Road, MS 341 Anchorage, Alaska 99503, USA

⁴Centre d'Ecologie Fonctionnelle et Evolutive, CNRS UMR 5175, 1919 Route de Mende, 34293 Montpellier, France

Many life-history traits are expressed interactively in life, but to a varying extent on different occasions. Changes in trait expression can be accounted for by differences in the quality of the environment ('environmental constraint' hypothesis) or by strategic adjustments, if the relative contribution of the trait to fitness varies with time ('strategic allocation' hypothesis). In birds, egg production is lower in replacement clutches than in first clutches, but it is unknown whether this reduction results from an environmental constraint (e.g. food being less available at the time when the replacement clutch is produced) or from a strategic allocation of resources between the two breeding attempts. To distinguish between these two hypotheses, we performed an experiment with black-legged kittiwakes (*Rissa tridactyla*). Pairs were either food-supplemented or not before the first clutch was laid onwards and we induced them to produce a replacement clutch by removing eggs once when the first clutch was complete. As predicted by the 'strategic allocation' hypothesis, egg production of food-supplemented and non-food-supplemented birds decreased between first and replacement clutches. This suggests that kittiwakes strategically reduce investment in egg production for their replacement clutches compared to first clutches.

Keywords: egg production; food availability; life-history evolution; parental investment; replacement clutch; reproductive strategies

1. INTRODUCTION

Trade-offs between life-history traits are ubiquitous since individuals have access to a limited amount of resources (Stearns 1992). To maximize fitness, individuals have to adjust the investment of resources in different life-history traits optimally, since allocation of resources in one trait is often made at the expense of another. An important consequence is that individuals are selected to invest more resources in traits that have a greater impact on fitness (Stearns 1992). A prime example is the impairing effect of reproductive effort on survival prospects (e.g. Stjernman *et al.* 2004). The resolution of this trade-off is modulated by environmental conditions, with one trait (e.g. survival) being favoured over the other (i.e. reproduction) when it has a disproportionate effect on fitness (Stearns 1992). Temporal variation in the quality of the environment is, therefore, an important factor to be considered in evaluating why life-history traits are expressed to various extents at different life stages. A common example is individuals reproducing at different rates in successive breeding attempts (Clutton-Brock 1988). This pattern of variation in reproductive output can be the outcome of temporal variation in the quality of the environment, with parents providing more care to offspring when food is plentiful. Here, the environment clearly acts as a constraint ('environmental constraint' hypothesis). A second, non-mutually exclusive hypothesis to explain

temporal variation in reproductive output is a strategic allocation of resources into competing breeding attempts. To illustrate this 'strategic allocation' hypothesis, we can imagine that birds allocate more resources to egg production for a first as compared to a replacement clutch (Hipfner *et al.* 1999) because the reproductive value of offspring commonly declines with hatching date, the potential laying of a replacement clutch is conditioned on the loss of the first one, and physiological constraints exist due to the cost of having already produced a first annual clutch. Thus, individuals should invest more resources in their first clutch and reserve a limited amount of resources for a replacement clutch should it be needed (Milonoff 1991; Martin 1995; Hipfner *et al.* 2001). In most cases, egg production, expressed as simultaneous investments in egg and clutch sizes, is lower in replacement than in first clutches (Runde & Barrett 1981; Brown & Morris 1996; Grand & Flint 1996; Wendeln *et al.* 2000; Hipfner *et al.* 2001; but see De Neve *et al.* 2004). In order to tease out whether this is due to environmental constraints and/or strategic allocation, an experimental approach is necessary as these hypotheses may work in concert under natural conditions.

To the best of our knowledge, there are no experimental studies that have tested whether this reduction in egg production results from a change in food supply and/or from a strategy evolved through natural selection. For this purpose, we conducted an experiment with the black-legged kittiwake (*Rissa tridactyla*) with the aim of determining whether the decrease in egg production for

* Author for correspondence (julien.gasparini@unil.ch).

a replacement clutch observed in natural conditions (Runde & Barrett 1981; Barrett 1989) occurs because at that time food resources become scarce ('environmental constraint' hypothesis) or because, independently of the food supply, birds strategically invest more effort in the first than in a replacement clutch ('strategic allocation' hypothesis). The kittiwake is a suitable model organism to address these issues because 60–92% of pairs that naturally lose their eggs produce a replacement clutch (Wooller 1980; Barrett 1989; Barrett 1996) and because food supply is known to boost egg production (Gill *et al.* 2002). These conditions imply that we can induce birds to replace a clutch, and furthermore that food supply is an important environmental factor affecting egg production.

We created two experimental groups in which individuals were food-supplemented or not during the production of both their first clutch and a replacement clutch. The latter was induced by removing the first clutch, thereby ensuring that we obtained an unbiased sample of birds, which failed at the first breeding attempt. In this experimental set-up, if egg production decreases between the first and replacement clutches in the two food treatments, we can conclude that kittiwakes strategically reduce investment in egg production. If egg production decreases only in non-food-supplemented pairs, it would imply that food was a limiting factor to keep investment in the replacement clutch at the same level as in the first attempt. If egg production decreases in the two food treatments, but more so in the non-food-supplemented pairs, then we can conclude that both hypotheses account for the seasonal decrease in egg production.

2. MATERIAL AND METHODS

The experiment was conducted in a kittiwake colony numbering about 12 000 pairs on Middleton Island (59°26' N, 146°20' W) in the northern Gulf of Alaska (Gill *et al.* 2002). Birds breed on cliffs and on several artificial structures, including an abandoned US Air Force radar tower that has been modified to provide highly accessible nest sites for experiments such as ours (Gill *et al.* 2002; Gill & Hatch 2002; Lanctot *et al.* 2003). Artificial nest sites created on the upper walls of this tower can be viewed from the inside of the building through sliding panes of one-way mirror glass.

In the spring of 2002, we allocated nests at random to two experimental groups, food-supplemented ($n=12$) and not supplemented ($n=13$) nests. As in a previous study using a comparable design (Lanctot *et al.* 2003), adult males and females from the treatment group were provided three times daily (08:00, 14:00 and 18:00 h) with capelin *Mallotus villosus* until satiation was reached. Capelins (average individual mass = 25 g), a high-quality natural prey of kittiwakes, were given through a hole in the wall in a way that kittiwakes could not see the researcher. Supplemental feeding began on 16 May and ended when the replacement clutch was complete. Food-supplemented birds were fed an average of 8.3 ± 1.0 days before they laid the first clutch (each bird consuming 18.8 ± 4.9 supplemental fish in total) and an average of 27.4 ± 0.8 days before they started to lay a replacement clutch (each consuming 69.33 ± 8.33 supplemental fish in total). Kittiwakes consumed a lower number of fishes per day before laying the first clutch (time period between first day of supplementation until the first egg was laid) than the replacement clutch (time period between the

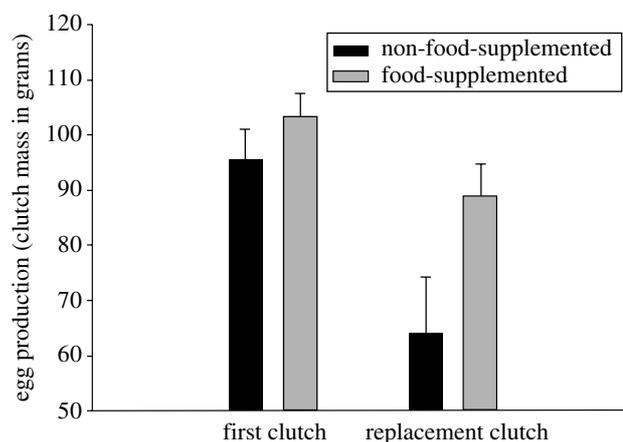


Figure 1. Mean egg production + standard error of food-supplemented ($n=12$) and non-food-supplemented pairs ($n=13$) in first and replacement clutches.

moment when we removed the first clutch and when the first egg of the replacement clutch was laid; 1.60 ± 0.38 versus 2.68 ± 0.27 ; paired t -test, $t_{11}=2.77$, $p=0.02$).

Both food-supplemented and non-food-supplemented pairs were monitored daily to determine laying date and nest contents. In both groups, we induced clutch replacement by removing eggs after the first clutch was complete, that is on an average 6.7 ± 0.5 days (range: 5–14) after the first egg of the first clutch was laid. This number of days was similar in the two experimental groups (Student t -test, $t_{23}=0.93$, $p=0.36$). Ninety eggs (first and replacement eggs pooled) from 25 nests were weighted with an electronic balance (0.1 g). For each clutch, we defined egg production as the sum of the mass of all eggs.

All analyses were conducted with SAS software (SAS Institute 1996). For all two-tailed statistical tests, the significance level was set at $p < 0.05$. Means are quoted \pm their standard error.

3. RESULTS

All 12 food-supplemented pairs and 11 of 13 non-food-supplemented pairs produced a replacement clutch 13.3 ± 0.6 days after their first clutch was experimentally removed. This time interval was not affected by the feeding treatment (Student t -test, $t_{21}=0.48$, $p=0.63$). Mean laying dates of first (24 May ± 1 day) and replacement clutches (14 June ± 1 day) did not differ between food treatments ($t_{23}=0.11$, $p=0.92$ versus $t_{21}=0.52$, $p=0.61$).

As predicted by the 'strategic allocation' hypothesis, egg production was lower in the replacement clutch compared to the first clutch in both non-food-supplemented (paired t -test, $t_{12}=2.29$, $p=0.041$) as well as in the food-supplemented treatment ($t_{11}=2.21$, $p=0.048$; figure 1). Egg production was higher when mothers were food-supplemented than non-food-supplemented and the decrease in egg production between the first and replacement clutch tended to be greater when kittiwakes were not fed (14.3 ± 6.5 g) compared to when they were food-supplemented (31.6 ± 13.8 g), but this difference was not significant (two-way ANOVA with egg production as the dependent variable and nest as a repeated effect nested within feeding treatment; interaction between clutch number and feeding treatment: $F_{1,23}=1.21$,

$p=0.28$; clutch number: $F_{1,23}=8.60$, $p=0.007$; feeding treatment: $F_{1,23}=7.05$, $p=0.01$; figure 1).

4. DISCUSSION

Although food supply significantly altered egg production, reduction in investment between the two successive clutches was detected in the two food treatments (figure 1). This indicates that, in kittiwakes, the decrease in egg production for replacement clutches, is not solely due to a constraining effect of food supply, as predicted by the 'environmental constraint' hypothesis, but rather to a reduction of maternal investment independently of food supply in a replacement clutch as compared to the first clutch, supporting the 'strategic allocation' hypothesis. Our test is conservative because, first, individuals had more time to accumulate resources via food supplementation for the replacement compared to the first breeding attempt. Second, the number of fishes consumed per day was on average higher during the time interval between the laying of the first and the replacement clutch than before the first clutch was laid. This difference in consumption rates supports the strategic 'allocation hypothesis' as egg production was reduced despite an increased rate of fish consumption which should have compensated for possible initial differences in nutritional states. The lack of significant difference between reduction in egg investment between the two breeding attempts in food-supplemented and non-food-supplemented birds does not exclude that the 'environmental constraint' hypothesis may also play a role. This is likely to be the case, especially as in accord with previous studies (Gill & Hatch 2002), we found that food supply altered egg production. The absence of a significant interaction between the feeding treatment and the clutch number may be due to the low power of our statistical analysis. Overall, the fact that both hypotheses are verified is interesting in the light of recent studies stressing that understanding population responses to environmental changes requires considering resource variability at different spatial and temporal scales and the adaptive responses of individuals (e.g. Petteorelli *et al.* 2005).

The strategic reduction in investment between the first and replacement clutch is not surprising because reproductive success declines with date, in term of both the number and quality of offspring as reported for kittiwakes (Coulson & Thomas 1985) and seabirds in general (Moreno 1998). Furthermore, because under natural conditions only a minority of pairs lose their eggs at the first breeding attempt and have, therefore, the need to produce a replacement clutch (around 35% on Middleton island in 1996 and 1997, see Gill & Hatch 2002), natural selection should favour individuals that invest most of their resources in the first breeding attempt, keeping only a limited amount of resources for an improbable replacement clutch. A physiological constraint could also limit the possibility to invest as much in the replacement clutch as in the first one due to some intrinsic decrease of resources that may not be possible to fully compensate via food supplementation (Bolton *et al.* 1992). However, this physiological cost of having produced a first clutch is in fact considered as participating in the strategic allocation of resources between the two successive breeding attempts. For instance, if the fitness benefit of producing

a replacement clutch were higher than the benefit derived from a first clutch (e.g. if food resources were higher later in the breeding season), then natural selection could favour mothers that allocate more energy in the replacement clutch than in first clutch despite the cost of having produced a first clutch (see Hubner *et al.* 2002 for a similar example). Previous experimental studies have demonstrated a strategic reduction of egg size when clutch size increased in gulls (Nager *et al.* 2000), but to our knowledge our study provides the first experimental evidence that the reduction of egg production observed in many birds between first and replacement clutches results from a strategic optimization of resources.

We thank N. Bargmann, P. Bize, M.-L. Gentes, C. Hand, B. Krolik, K. D. McCoy, R. Milligan, and M. Tierney for help at various stages of the study. We also thank the referees for comments on first versions of the manuscript. This work benefited from support by the French Polar Institute (IPEV; programme no. 333), the CNRS, the French Biodiversity Institute (IFB) and the US Geological Survey. We also thank the personnel of the US Federal Aviation Administration stationed on Middleton Island for providing us with logistical support. Permits to manipulate nest contents of kittiwakes were granted by the US Fish and Wildlife Service. AR was financed by the Swiss National Science Foundation (grant PP00A—102913). J.G. was supported by a Ph.D. fellowship from the French Ministry of Research and by the SNF (grant PP00A—102913 to A.R.).

REFERENCES

- Barrett, R. T. 1989 The effect of egg harvesting on the growth of chicks and breeding success of the shag *Phalacrocorax aristotelis* and the kittiwake *Rissa tridactyla* on Bleiksoy, North Norway. *Ornis. Fenn.* **66**, 117–122.
- Barrett, R. T. 1996 Egg laying, chick growth and food of kittiwakes *Rissa tridactyla* at Hopen, Svalbard. *Polar Res.* **15**, 107–113.
- Bolton, M., Houston, D. C. & Monaghan, P. 1992 Nutritional constraints on egg formation in the lesser black-backed gull: an experiment. *J. Anim. Ecol.* **61**, 521–532.
- Brown, K. M. & Morris, R. D. 1996 From tragedy to triumph: renesting in ring-billed gulls. *Auk* **113**, 23–31.
- Clutton-Brock, T. H. 1988 *Reproductive success. Studies of individual variation in contrasting breeding systems*. Chicago, IL: University of Chicago Press.
- Coulson, J. C. & Thomas, C. 1985 Differences in the breeding performance of individual Kittiwake gulls, *Rissa tridactyla* (L.). In *Behavioural ecology: ecological consequences of adaptive behaviour* (ed. R. M. Sibly & R. H. Smith), pp. 489–503. Oxford, UK: Blackwell Scientific Publications.
- De Neve, L., Soler, J. J., Soler, M. & Pérez-Contreras, T. 2004 Differential investment counteracts for late breeding in magpies *Pica pica*: an experimental study. *J. Avian Biol.* **35**, 237–345. (doi:10.1111/j.0908-8857.2004.03161.x)
- Gill, V. A. & Hatch, S. A. 2002 Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. *J. Avian Biol.* **33**, 113–126. (doi:10.1034/j.1600-048X.2002.330201.x)
- Gill, V. A., Hatch, S. A. & Lanctot, R. B. 2002 Sensitivity of breeding parameters to food supply in black-legged kittiwakes *Rissa tridactyla*. *Ibis* **144**, 268–283. (doi:10.1046/j.1474-919X.2002.00043.x)
- Grand, J. B. & Flint, P. L. 1996 Renesting ecology of northern pintails on the Yukon–Kuskokwim delta, Alaska. *Condor* **98**, 820–824.

- Hipfner, J. M., Gaston, A. J., Martin, D. L. & Jones, I. L. 1999 Seasonal declines in replacement egg-layings in a long-lived, Arctic seabird: costs of late breeding or variation in female quality? *J. Anim. Ecol.* **68**, 988–998. (doi:10.1046/j.1365-2656.1999.00346.x)
- Hipfner, J. M., Gaston, A. J. & Storey, A. E. 2001 Nest-site predicts the relative investment made in first and replacement eggs by two long-lived seabirds. *Oecologia* **129**, 234–242. (doi:10.1007/s004420100731)
- Hubner, C. E., Tombre, I. M. & Erikstad, K. E. 2002 Adaptive aspects of intraclutch egg-size variation in the high arctic barnacle goose (*Branta leucopsis*). *Can. J. Zool.* **80**, 1180–1188.
- Lanctot, R. B., Hatch, S. A., Gill, V. A. & Eens, M. 2003 Are corticosterone levels a good indicator of food availability and reproductive performance in a kittiwake colony? *Horm. Behav.* **43**, 489–502. (doi:10.1016/S0018-506X(03)00030-8)
- Martin, T. E. 1995 Avian life history evolution in relation to nest sites, nest predation and food. *Ecol. Monogr.* **65**, 101–127.
- Milonoff, M. 1991 Renesting ability and clutch size in precocial birds. *Oikos* **62**, 189–194.
- Moreno, J. 1998 The determination of seasonal declines in breeding success in seabirds. *Etologia* **6**, 17–31.
- Nager, R. G., Monaghan, P. & Houston, D. C. 2000 Within-clutch trade-offs between the number and quality of eggs: experimental manipulations in gulls. *Ecology* **81**, 1339–1350.
- Pettorelli, N., Mysterud, A., Yoccoz, N. G., Langvatn, L. & Stenseth, N. C. 2005 Importance of climatological down-scaling and plant phenology for red deer in heterogeneous landscapes. *Proc. R. Soc. B* **272**, 2357–2364. (doi:10.1098/rspb.2005.3218)
- Runde, O. J. & Barrett, R. T. 1981 Variations in egg size and incubation period of the kittiwake *Rissa tridactyla* in Norway. *Ornis. Scand.* **12**, 80–86.
- SAS Institute 1996 *SAS procedures guide, version 6.1*. Cary, NC: SAS Institute Inc.
- Stearns, S. C. 1992 *The evolution of life histories*. Oxford, UK: Oxford University Press.
- Stjernman, M., Raberg, L. & Nilsson, J. A. 2004 Survival costs of reproduction in the blue tit (*Parus caeruleus*): a role for blood parasites? *Proc. R. Soc. B* **271**, 2387–2394. (doi:10.1098/rspb.2004.2883)
- Wendeln, H., Becker, P. H. & González-Solís, J. 2000 Parental care of replacement clutches in common terns (*Sterna hirundo*). *Behav. Ecol. Sociobiol.* **47**, 382–392. (doi:10.1007/s002650050681)
- Wooller, R. D. 1980 Repeat laying by kittiwakes *Rissa tridactyla*. *Ibis* **122**, 226–229.