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Ligature use in food studies of precocial birds — methodological results from Antarctic skua chicks

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This paper is the first methodological investigation of the ligature application for food studies in semi-precocial birds. In a population of Brown Skuas, South Polar Skuas and mixed pairs, ligatures were attached to chicks for a period of 28 hours. Of 408 theoretical sampling visits, 8% could not be carried out. The number of times the ligature was applied did not cause differences in mortality of chicks nor did I find a growth difference for treated and untreated chicks. The method did not work equally well for three skua forms with different diets. Parent birds disgorged food equally often to ligatured and control chicks. This method is probably less accurate when used for diets with a high proportion of fish. While I was applying the ligature, body weight loss showed a non-linear decline, with a drop appearing in the first hours after application. The chicks may compensate for weight loss. In chicks whose stomachs were flushed after ligature use, no food was found, leading to the assumption that the ligature method is highly efficient. A projection of the total food consumption by field data revealed values of only 45% (Brown Skua) and 25% (South Polar Skua) of that of the model by Drent and others (1992). The advantages and disadvantages of ligaturing are discussed in regard to its further use in precocial birds.

1. Introduction

The ligature method for analysis of food composition and consumption has been used for food studies in passerines (Kluyver 1933, Grün 1972, Johnson et al. 1980, Strebel 1991, Pascual & Peris 1992, Sánchez-Alonso et al. 1996) and woodpeckers (Raquez & Ruge 1994). The findings of Grün (1972) and Johnson et al. (1980), showing that ligature application can reduce the number of feedings by 50% and 20%, respectively, gave grounds for concern. Johnson et al. (1980) estimated that control birds received seven times as much food in terms of volume as ligatured birds. In precocial birds, this technique has been previously employed only once (White et al. 1984), although without yielding any methodological results.

The aim of the present paper is to investigate the efficiency, accuracy, and impact of this method in semi-precocial, apparently relatively robust birds, the South Polar Skuas *Catharacta maccormicki*, the Brown Skua *Catharacta antarctica lonnbergi* and mixed pairs of both species. During the investigation period, the three forms differed considerably in their diets (Reinhardt 1997). This enables us to assess the ligature method for different diets.

2. Material and methods

The study was conducted on Potter Peninsula (62°14′S, 58°40′W), King George Island, in the maritime Antarctic. The ice-free area was about 8.6 km^2, 3.8 km^2 of which were covered by lichens and mosses. In the 1993–1994 season, the peninsula served as a breeding ground for 85 skua pairs (35 Brown Skuas, 40 South Polar Skuas and 10 mixed pairs) and in the 1994–1995 season, 77 pairs (29 Brown Skuas, 41 South Polar Skuas and 7 mixed pairs) were recorded. Fledgling weights of the three forms derived from logistic regressions for $t = 60$ days (K. Reinhardt unpubl.) were 1 765 g, 1 460 g, and 1 483 g, respectively.

In the austral summer 1993–1994, 16 Brown Skua chicks, 17 South Polar Skua chicks and 4 mixed-pair chicks were ligatured. They were weighed before and after the ligature procedure, and the weight change was recorded. All non-ligatured chicks served as a control group. I followed the fate of the chicks nearly until fledging and later compared mortality rates.

The ligature was a hemp string about 2 mm thick. The loop was closed by a plastic tube about 5 to 8 mm in length and 4.5 mm in diameter. The ligature was positioned around the neck as far down as possible towards the shoulders, until reaching the point where the oesophagus bends more inside the body. In this way, the chick is prevented from swallowing food, but not from breathing. In 1993–1994, I left ligatures on nestlings for 28 hours, from 12:00 until 16:00 the next day, local time. Hereafter, this period is referred to as an experimental period (EP). I controlled the ligatured chicks every four hours, each of these periods is referred to as an experimental interval (EI). Hence, each EP generally comprises eight EIs. In the laboratory, the prey items were sorted out by hand and their wet weights measured to the nearest 0.1 g (Sartorius MC 1 Analytic AC 120 S electronic balance).

In 1994–1995, one Brown Skua, ten South Polar Skuas and two mixed-pair chicks were ligatured for 12 hours. As the result of an early departure, the breeding could not be followed completely, and a mortality comparison was impossible. All procedures, including EI and weight change recording were the same as for the 1993–1994 season.

From preliminary observations of the foraging frequency, a 4-hour EI was thought to be sufficiently accurate in that one ligature sample was assumed to represent one meal size. The average feeding rates were independent of chick age (Reinhardt 1997). Feeding rates were 3.4 times per day for the Brown Skua, 2.8 times for the South Polar Skua and 1.3 times for mixed pairs (Reinhardt 1997). As chicks grew, meal size increased for all three skua forms (Reinhardt 1997).

I calculated a total consumption figure by summing up average meal sizes from ten-day-periods (see fig. 2 in Reinhardt 1997). In order to prove the efficiency of the method, I compared this value with the consumption estimate predicted by Drent et al. (1992): $ME = 35.15*M^{1.015}$, where ME is the total metabolisable energy needed to fledge, and M is the fledging body mass. The average of metabolisable energy was derived from the following sources — Krill: 3.7 kJ/g wet weight (Davis et al. 1989), Fish: 6.3 kJ/g wet weight (Davis unpubl. in Young (1994) for *Pleuragramma antarcticum),* penguin chick: 7.1 kJ/g wet weight (average value for a 2-kg chick, Myrcha & Kaminski 1982). All other items were given average density values in the calculation. Average energy densities of the food were 6.38 kJ/g wet weight, 6.13 kJ/g wet weight, and 6.42 kJ/g wet weight for the Brown Skua, the South Polar Skua, and for the mixed pairs, respectively (for the food spectrum of the respective season see Reinhardt (1997)).

In order to measure the impact of the number of ligature applications, fourteen chicks were treated a second time, with a minimum period of 20 days between the first and the second EP. For the analysis of the impact of species, treatment and species × treatment on mortality rates, I used a loglinear logit model (Norušis 1993).

To see whether ligatured chicks were able to compensate for weight loss, I compared weight gains from ligatured and control chicks. In 1993–1994, the growth curve followed a straight line from day 10 to day 35 after hatching (K. Reinhardt unpubl.). Thus, the weight gain during this period measured directly before ligaturing and within the next 5 to 25 days thereafter should not differ from the weight gain of control chicks. First-hatched chicks differ in their growth rate from second-hatched ones, but not from single chicks of a brood. I therefore compared first-hatched and single chicks together and second-hatched chicks separately.

In order to examine whether adult birds are reluctant to feed ligatured chicks, the frequency by which food was disgorged was examined in the austral summer 1994–1995. On 16 January 1995, five non-ligatured chicks were observed over a period of 8 hours, from 14:45 to 22:45 local time. Exactly 24 hours later, the same chicks were ligatured and the disgorging feeding frequencies recorded over the same time period.

For the test of ligature leakiness, six chicks (4 Brown Skuas, 1 South Polar Skua, and one mixed-pair chick) were stomach-flushed by the water-offloading technique (Wilson 1984) immediately after the removal of their ligatures on 19 January 1995. Additionally, the stomach contents of five non-ligatured chicks weighing between 450 g and 930 g were emptied by the water-offloading technique. Afterwards, the chicks were ligatured and their parents were fed with fish and meat. Four hours later, the chicks were captured again, and the contents of the ligatures were collected. After removing the ligature string, the chicks were stomach-flushed again.

Skua chicks naturally keep food for some time in the throat before swallowing (throat load). To see whether ligature loads differed from natural throat load, I compared the mean throat load from 12:00 the first day (before ligaturing) with that from 12:00 the second day. I also compared ligature load at 16:00 the first day with that at 16:00 the second day to ascertain the effects of ligature duration on the ligature load.

3. Results

3.1. The effects of ligatures on chicks

In total, 51 EPs (37 chicks) were carried out, in theory representing 408 EIs. In 32 EIs (7.7%) sampling was impossible for the following reasons:

- searching was terminated when the chick was not found after thirty minutes search time (6 EIs)
- sampling was terminated because of the earlier death of the chick (5 EIs)
- midnight sampling was not carried out for the observer's own security (9 EIs)
- the whole EP was aborted because of extreme weather conditions (12 EIs)

In four EIs, sampling was impossible after two chicks were preyed upon (presumably by other skuas). The remaining EI concerns a chick that was not found by the observer in the final control after more than four hours of intensive searching. It could therefore not be liberated from the ligature and was found dead the next morning. Thus, except for the four EIs where the chicks fell prey to other skuas, the reasons for EIs not being carried out were the observer's responsibility. Thus, the methodology caused the death of one chick (2.5% of the ligatured chicks, 1.9% of all EPs).

The number of times an adult disgorged food to the chicks did not change as a result of ligature application. There were no differences for five chicks before and after ligaturing (Wilcoxon matched pair test, $Z = -0.54$, n.s.).

When comparing the growth (Table 1), no difference in the mean slope during the linear growth phase (day 10–35) was apparent for ligatured compared with control chicks in the Brown Skua (Mann-Whitney $U_{6,14} = 38.5$, n.s.) and the South Polar Skua (Mann-Whitney $U_{2,19} = 19.0$, n.s). When considering only first and single chicks (that are possibly in better condition) in the Brown Skua, there were still no differences between ligatured and control chicks (Mann-Whitney $U_{5,9} = 22.0$, n.s.).

The analysis of the saturated logit model did not reveal any significant effects of species and treatment number on mortality rates (Z-values for parameter estimates ranging from -0.92 to 0.88, see also Table 2). Therefore, I applied an equiprobability model with the null hypothesis of equal mortality rates for all species-treatment combinations. This model fits the data, the null hypothesis cannot be rejected (likelihood ratio $\chi^2_8 = 9.179$, $p = 0.327$).

3.2. The efficiency and accuracy of the ligature method in the analysis of diet

Table 3 shows the number of controls during which food was found. The difference between the skua forms was significant ($\chi^2_2 = 51.87$, $P < 0.001$). Since this may reflect both different feeding activities and different ligature efficiencies in each skua form, Table 4, in addition, gives the percentage of chicks that lost weight during ligature application. Again, the difference between the skua forms was significant ($\chi^2_2 = 6.54$, $P < 0.05$).

Considering only chicks with a negative weight development during one EP, there was a mean weight loss of 11.8% (s.d. = 7.1%, range 2.3–28.1%) of the body weight in 28 hours for the Brown Skua. The weight loss of South Polar Skua chicks averaged 4.8% (s.d. = 3.4%, range 0.5–10.7%), and that of the mixed-pair chicks was between 3.6% and 8.3%. There was no correlation between weight loss and body-weight in Brown Skua chicks (Spearman rank $r_{24} = -0.22$, n.s.) nor in South Polar Skua chicks (Spearman rank $r_{15} = -0.23$, n.s.). During the 12-hour periods of ligature application in the 1994–1995 season, weight changes of one Brown Skua chick, ten South Polar Skua chicks and two mixed-pair chicks could be obtained. The Brown Skua chick lost 6.6%, the mixed pair chicks 8.3% and 10.2% of their body weights in 12 hours. Two of the South Polar Skua chicks did not lose weight. The remaining eight lost 1.5% to 9.8% (mean 5.3%, s.d. = 3.4%) of their body weight in 12 hours.

There was no difference in the percentage weight loss for 12 hours and 28 hours of ligature application (Mann-Whitney $U_{8,14} = 54.5$, n.s.) for the South Polar Skua. Also, the weight loss of the Brown Skua chick ligatured for 12 hours was within the range of weight loss during the 28-hour application. The two 12-hour samples from the mixed-pair chicks were slightly higher than the respective values from the 28-hour procedure.

Food was not found in any of the six chicks that were controlled by the water-offloading technique after ligature application, except for small pieces of penguin feathers, algae, lichens, or stones. In two of the chicks, food had been found during the previous ligature control. Out of the five chicks that were water-offloaded before and after a four-hour ligature use, two had been fed by their parents with 67 g and 31 g, respectively. None of the chicks had material in their stomachs except for pieces of feathers, fish scales, or lichens.

The mean throat loads found at 12:00 the first day (mean 52.8 g, s.d. = 60.2) did not differ from that found at 12:00 the second day (mean 31.8 g, s.d. = 24.5) for the Brown Skua (Wilcoxon's test $W_{3,24} = 144.0$, n.s) and the South Polar Skua (mean 8.9 g, s.d. = 5.1 vs mean 10.8 g, s.d. = 11.4, $W_{6,5} = 28.0$, n.s.). The time of day at which the ligature was attached to a bird did not influence the results. Mean ligature loads did not differ between the EIs at 16:00 the first and the second day for the Brown Skua (17.6 g *vs* 24.2 g, $W_{13,16} = 175.0$, n.s.) and the South Polar Skua (6.8 g vs 2.8 g, $W_{7,4} = 17.0$, n.s.).

Using the formula from Drent et al. (1992) and the calculated average energy density of the food (see Methods), Brown Skua chicks should have received 10,878 g, South Polar Skua chicks 9,339 g, and mixed-pair chicks 9,059 g in one fledging period. However, a cumulative addition of the average daily food amount (as calculated from ligature loads) up to day 60 reveals a consumption of only 4.922 g of food for a Brown Skua chick and 2.396 g for a South Polar Skua chick.

4. Discussion

For the first time, this paper reports on the impact and efficiency of the ligature method in precocial

Table 1. Mean weight gain of different skua chick categories during the linear growth phase.

Chick category	N	Mean growth rate (g/ day) ± s.d.
First-hatched and single Brown Skua — ligatured	5	40.48 ± 6.88
First-hatched and single Brown Skua — control	9	40.20 ± 8.63
Second-hatched Brown Skua — ligatured	1	33.33
Second-hatched Brown Skua — control	5	40.63 ± 7.32
All Brown Skua — ligatured	6	39.29 ± 6.81
All Brown Skua — control	14	40.35 ± 7.90
First-hatched and single South Polar Skua — ligatured	2	36.55
First-hatched and single South Polar Skua — control	19	37.39 ± 5.26

birds. In total, 7.7% of all sampling visits were impossible, making the investigation of food changes within a day more difficult, since percentage data of positive controls will have to be applied (Reinhardt 1997). However, in regions with less extreme weather conditions, this figure can probably be reduced and the applicability of the method improved. One chick was killed owing to the inability of the observer to locate the chick at the final EI. Two chicks were preyed upon by other skuas. Even when these three chicks are included in the analysis, no mortality differences were detected between ligatured and non-ligatured skua chicks.

Pascual and Peris (1992) found mass differences between ligatured and non-ligatured 14-day-old starlings, depending on the duration of application. However, their study says nothing about the chicks' ability to compensate for weight loss later in the season. During ligaturing, skua chicks usually lost weight. There was no difference in the weight loss of chicks that were ligatured for 12 hours or 28 hours. The decline is therefore not a linear process. The weight drop is likely to occur within the first hours after ligature application and can probably be attributed primarily to digestion and defecation of food items that were already in the stomach. There appeared to be no physiological damage to the skua chicks during the 28 hours of application. The weight drop is compensated for within a few days, as was shown by the similar growth rates of control chicks and chicks weighed before and some days after ligature application in the linear growth phase. The similar growth rates of the chicks, as well as the equal food disgorging rates before and after ligaturing, in turn led to the assumption that there are no differences in the total food mass delivered to ligatured and non-ligatured chicks. Johnson et al. (1980) estimated that the volume of food received by ligatured chicks of two passerine species was up to seven times less than that calculated for non-ligatured chicks. In two other passerine species, Grün (1972) found a lower number of feeding flights to nests with ligatured chicks than to nests with control chicks. Grün (1972) and Johnson et al. (1980) point out that the results also have a bias in the qualitative data, since larger food items are more easily disgorged by the chicks and sometimes taken by the parents themselves. Passerine birds, however, beg for food by gaping, whereas skua chicks squeal for food when the adult arrives. Gaping usually causes gasping in ligatured chicks (Johnson et al. 1980) and, therefore, prevents the adults from feeding the chick. In this study, no evidence has been found that ligatures affect squealing in skua chicks in a way that would inhibit the adults feeding the chicks.

Although there were no behavioural alterations and no differences in mortality for either species or treatment, food consumption projections carried out on the basis of average meal sizes and the number of foraging trips revealed values as low as 45.2% for the Brown Skua and 25.7% for the South Polar Skua, in comparison to theoretical considerations by Drent et al. (1992). One might think of two reasons for this deviation. First, taking into account the high variability in fledging weight, a 100 g lower fledging weight would result in a roughly 10% lower theoretical consumption estimate. Second, in a few cases, all EIs were positive during an EP. Thus, the maximum feeding rate detected by this method was 8 per EP, or

Table 2. Survival until fledging of skua chicks that were treated with ligatures once, twice, or not at all.

	Number of ligature treatments		
	0	1	2
Brown Skua			
Chicks alive	6	8	3
Chicks dead	11	8	5
South Polar Skua			
Chicks alive	24	9	2
Chicks dead	10	8	3
Mixed pairs			
Chicks alive	5	2	1
Chicks dead	3	2	0

Table 3. Number of ligature sampling visits during which food was found (= successful visits) in three different skua forms.

	Total no. of sampling visits	No. of successful visits (%)
South Polar Skua	175	48 (27.4%)
Brown Skua	188	116 (61.7%)
Mixed pairs	21	10 (47.6%)

6.9 per 24 hours. A potential higher feeding rate, especially in territorial birds (Pietz 1986) would remain undetected, and subsequently lower the mean value of feeding rate. A lower mean feeding rate would then result in a lower total consumption estimate.

In the study area, the skua forms differ considerably in their diet. More than 90% of the Brown Skua's food consists of penguin meat and station garbage, and only 2% of fish. The analysis of the South Polar Skua food items, in contrast, yields a 95% content of fish and amphipods, and hardly any penguin meat. The mixed-pair chicks are fed with 80% marine food and 20% penguin meat (Reinhardt 1997). In comparison to other studies, Reinhardt's (1997) study revealed the highest proportion of fish ever found in skua diets (K. Reinhardt unpubl.) except for the stomach flushing study by Montalti et al. (1996). Reinhardt (1997) suggested that the ligature method would be more sensitive than any other method for the estimation of the proportion of fish in the diet. However, 25% of the South Polar Skua chicks did not lose weight during the 28-hour ligature application (20% during the 12-hour period), thus the method did not work in at least 25% of the chicks. In contrast, only one (4%) of the Brown Skua chicks did not loose weight. This suggests an influence of the proportion of fish on the accuracy of the method, possibly caused by the slipperiness of the fish items. This would mainly explain differences between the skua forms but would not explain the differences from the model by Drent et al. (1992).

In conclusion, the ligature method is applicable but has certain advantages and disadvantages.

Table 4. The number of skua chicks that lost weight during ligature application as a measurement of the efficiency of the method.

	No. of chicks surveyed	No. of chicks with weight loss (%)
1993–1994 (28 hours)		
South Polar Skua	24	18 (75%)
Brown Skua	27	26 (96%)
mixed pairs	6	4 (67%)
1994–1995 (12 hours)		
South Polar Skua	10	8 (80%)

The ligature method is not costly and is only moderately time consuming. It possibly gives no artificial throat loads and is repeatable. In skuas, it does not affect mortality and has only a short-term impact on the growth pattern. Despite weight loss, the chicks are probably not pathologically affected in their growth. The ligature method enables a fairly exact detection of diet composition and the calculation of detailed, wet or dry weight based, energy density data of the food. However, even with experience, sampling may at times be impossible for several reasons which will introduce additional variance into the data set and make the statistical conclusions less powerful. Regular sampling enables the detection of diel feeding patterns, if there are any. A very detailed knowledge of nest positions and chick hiding places is necessary, however, if the method is to be applied during an investigation period that continues past daylight. Despite good knowledge of the local conditions, chick loss owing to the direct impact of the ligature cannot be ruled out when the chick is not found at the final control. For the quantitative calculation of food consumption, a correction factor has to be determined depending on the percentage of fish in the diet, and possibly for different populations, as well. There were no diet differences between EPs of 28 and 12 hours (shown as the similarity between the 1993–1994 and 1994–1995 study period — Reinhardt 1997). Therefore, I suggest a combination of the consumption model by Drent et al. (1992) and the use of energy density data from a ligature study. For ethical reasons, the shortest possible experimental period should be used and chicks should be treated only once. Finally, this study also attempts to encourage researchers to seek out alternative methods of feeding ecology, since the death of a chick, as reported here, can never be ruled out completely (and in many cases may be found in unpublished field diaries).

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Selostus: **Kaulasiteen käytön soveltuvuus pesäpakoisten lajien ravintotutkimuksiin — tutkimus Etelämantereen kihulajeilla.**

Poikasille asennettavia kaulasiteitä on käytetty laajasti tutkittaessa lintujen poikasajan ravintoa. Kaulaside estää poikasia nielemästä emojen niille tarjoamaa ruokaa, jolloin tutkijalla on mahdollisuus tarkastaa ravinnon koostumus. Joissakin aiemmissa tutkimuksissa on todettu kaulasiteen käytön vähentävän poikasten saaman ravinnon määrää, vaikka tutkija kompesoisikin kaulasiteistä poistamansa ravinnon poikasille. Kirjoittaja tutki poikasille asetettavan kaulasiteen soveltuvuutta pesäpakoisten kihulajien (etelänkihu ja etelämantereenkihu) ravintotutkimukissa ja arvioi samalla menetelmän tehokkuutta ja tarkkuutta. Kaulaside asetettiin yhteensä 50 poikaselle kahden pesimäkauden aikana. Neljälletoista poikaselle side asetettiin toistamiseen 20 päivää ensimmäisen koekerran jälkeen. Side oli paikallaan 28 tuntia kerrallaan. Sillä, kuinka usein poikanen osallistui kokeeseen, ei ollut minkäänlaista yhteyttä elossasäilyvyyteen. Kokeeseen osallistuneiden poikasten kasvu ei myöskään poikennut kontrollipoikasten kasvusta. Emot ruokkivat kaulasiteellä varustettuja ja kontrollipoikasia yhtä usein. Useat poikaset menettivät painoaan kaulasiteen ollessa paikoillaan siten, että suurin osa painon menetyksestä tapahtui muutaman tunnin aikana heti siteen asentamisen jälkeen, mutta poikaset kykenivät kompensoimaan painonmenetyksen kokeen jälkeen. Menetelmä ei kuitenkaan sopinut yhtä hyvin kaikille kihuille, sillä 25% etelämantereenkihun poikasista eivät menettäneet yhtään painoa. Tämä kertoo siitä, että kaulaside ei ainakaan kokonaan estänyt tämän lajin poikasia saamasta ravintoa. Kirjoittaja toteaa, että menetelmä ei ole aivan niin tarkka kihulajeille, joiden ravinnosta kalat muodostavat suuren osan. Yhdeltäkään poikaselta ei kokeen jälkeen huuhdeltaessa kuitenkaan löytynyt ravintoa mahasta, mikä todistaa, että kaulaside on tehokas menetelmä ravintotutkimuksiin.

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