INTRASPECIFIC VARIATION IN LENGTH OF INCUBATION PERIOD IN AVOCETS *RECURVIROSTRA AVOSETTA*

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This paper investigates factors influencing the intraspecific variability of incubation periods in Avocets *Recurvirostra avosetta*. The length of the incubation period of 278 clutches ranged from 19 to 34 days with an average of 23.1 days. Incubation period was influenced by clutch size. There was a seasonal decrease in incubation period resulting in a difference of 1.7 days between the earliest and the latest clutches. The seasonal trend could not be explained by ambient temperature. No relationships could be found between incubation period and colony size, nest density, or habitat. There were significant positive correlations between incubation period and bill length and foot length of the neonates. The possibility that incubation period is influenced by a trade-off between egg and chick mortality rates and embryonic and chick growth rates is discussed.

Key words: *Recurvirostra avosetta* - breeding biology - incubation - colony breeding - growth - life-history - reproductive success

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INTRODUCTION

Interspecific variation in the length of incubation period in birds has attracted considerable attention. Among selective factors that may influence the evolution of the length of incubation period, or the length of embryonic development, are incubation temperatures, predation rates and requirement for advanced development at hatching (Heinroth 1922; Worth 1940; Nice 1954; Vleck *et al.* 1980; Rahn & Ar 1984; Nol 1986; Starck 1993). Incubation periods are not only different between species but can also show a high variability within species (Drent 1975). Factors like egg mass, clutch size, laying date, and ambient weather conditions have been found to influence the length of the incubation period (MacRoberts & MacRoberts 1972; Parsons 1972; Bryant 1975; Nisbet & Cohen 1975; Martin & Arnold 1991; Székely *et al.* 1994; Murphy 1995; Yogev *et al.* 1996).

Avocets *Recurvirostra avosetta* are colonial shorebirds nesting on open ground. As for many other open nesting bird species (Ricklefs 1969), predation of eggs is the most important reason of failure of Avocet clutches. Flooding of nests is the second most important mortality factor (Glutz von Blotzheim *et al.* 1977; Cramp & Simmons 1983; H. Hötker unpubl. data). Both predation and inundation are risks that increase with length of exposure. Thus, for assessing hatching success and factors associated with hatching success, detailed knowledge of incubation periods is needed. The first aim of this paper is to investigate whether there are individual differences in the length of the incubation period of Avocets that must to be taken into account when using Mayfield's formula for calculating hatching success (Mayfield 1961).

The length of the incubation period is not only important for considering the mortality risk of eggs or clutches, but it may also affect the degree of maturity of neonates. In general longer incubation periods are associated with higher degrees of maturity at hatching (Nice 1954). A higher risk of mortality in the egg-phase due to a longer incubation period might be compensated by a more advanced development of the neonate. This could happen if more mature neonates need less time to reach the fledgling stage and, therefore, experience a lower risk of mortality as chicks than do less developed neonates. If this is the case, Avocets should adjust their incubation periods according to the trade-off between the daily mortality risk between egg- and chick-phases. Relatively lower daily egg-mortality rates than daily chick-mortality rates should favour long incubation periods. For Avocets there is no published information on the relationship between incubation period and degree of development. The second aim of this paper, therefore, is to investigate whether longer incubated Avocet eggs produce more mature hatchlings.

Avocets may be the subject of intra-specific nest parasitism (Emeis 1930; Glutz von Blotzheim *et al.* 1977; H. Hötker unpubl. data). One of the possible costs of nest parasitism to the host is a less effective incubation of the enlarged clutch (Yom-Tov 1980; Anderson 1984) which could result in a longer incubation time (Székely *et al.* 1994; Yogev *et al.* 1996). As some of the nests in this study were obviously parasitised, the possibility of incubation periods in Avocets being affected by intraspecific nest parasitism could be tested.

STUDY SITES AND METHODS

Data on the lengths of incubation periods were collected for 278 Avocet nests at two sites on the Wadden Sea coast of Schleswig-Holstein in Germany between 1988 and 1996. The Beltringharder Koog (54°22'N, 8°57'E) and the Fahretofter Westerkoog (54°42'N, 8°48'E) are recent land-claims where Avocet colonies were situated on small islands and beaches within these polders, and on saltmarsh outside the polders.

Avocets usually have clutches of four eggs (mean ± SD clutch size in the study site 3.72 ± 0.79, *n* = 2483), which are incubated by both parents. Avocets are supposed to start incubation after the laying of the third or the fourth egg of a clutch (Glutz von Blotzheim *et al.* 1977). In these study sites some pairs, however, started incubation with their first or second egg (H. Hötker unpubl. data). The time parents spent sitting on their eggs could not be precisely measured. In order to keep data comparable between nests, Drent's (1975) definition of incubation period, the number of days between the deposition of the last egg of a clutch and the hatching of the last chick, was was used.

All the 278 nests involved in this study were found before or during the egg-laying phase and were controlled at hatching. In most cases the date of laying of the last egg had to be estimated by assuming that one egg is deposited each day, and that there is a break of one day without laying between the third and fourth eggs. This pattern fits with observations of laying patterns, and a five day period of a completion of a four egg clutch (Glutz von Blotzheim *et al.* 1977; H. Hötker unpubl. data). The hatching of the last chick could often be directly observed. If hatching had started in a clutch, but the last successful egg was still completely intact, the last chick was assumed to hatch the following day.

To assess the effect of incubation period on neonate development, the biometric data of 102 chicks that hatched from 4-egg clutches with known incubation period were analysed. All chicks were measured within 24 h after hatching. Body mass was recorded with Pesola spring balances to the nearest 0.1g. The mass of the metal ring (1.89 g) is included in the mass. Bill lengths were measured by calipers to the nearest 0.1mm, and foot lengths (tarsus and middle toe without claw) were taken with a stopped ruler to the nearest 1 mm.

Daily survival rates of eggs were calculated according to Mayfield (1961), using data from 3294 nests. Chick survival was estimated by dividing the number of fledged chicks (directly counted in the field) by the number of hatchlings (estimated from the known number of nests and the hatching success). Daily chick survival rate was calculated by assuming a constant chick mortality rate throughout the chick period, using 37 days as the length of the fledgling period (Glutz von Blotzheim *et al.* 1977; H. Hötker unpubl. data). I distinguished between early broods (clutch initiation in the first half of the breeding season, i.e. before 20 May, fledging of chicks before 20 July) and late broods (all other broods).

Weather data (daily mean values of air temperature and wind velocity, daily totals of rainfall and sunshine hours) came from the Deutsche Wetterdienst, weather station Wyk on the island of Föhr (54°42'N, 8°33'E). Means of air temperature, wind velocity, amount of daily rainfall, and daily number of sunshine hours were calculated for the incubation period of each nest. The strong intercorrelation of all weather parameters (Pearson correlation coefficients between 0.302 and 0.776) precluded treating them as independent variables. For simplicity only air temperature (from here on called ambient incubation temperature) was used for statistical analyses.

The density of 48 colonies was measured as the mean of the distance between each nest and its nearest neighbour. Colonies were classified according to the following nest distance categories: 0.5 m - 1 m, 1.01 m - 2 m, 2.01 m - 4 m, 4.01 m - 8 m, 8.01 m - 16 m, >16 m. Colony size was defined as the total number of nests on a colony site. Two habitats were distinguished for analyses: saltmarsh (under influence of the tide) and polder (without tidal influence). All statistical treatments except calculations of hatching success were perfomed with SYSTAT 5.2 for Macintosh computers (Wilkinson *et al.* 1992). Survival rates of nests were compared using Johnson's (1979) test.

RESULTS

The lengths of successful incubation periods ranged between 19 days and 34 days (mean ± SD = 23.1 ± 1.6 days, median 23 days, n = 278). The lengths of more than 97% of all recorded incubation periods were between 20 days and 26 days (Fig. 1). The longest incubation periods (34 days and 30 days) were found with two exceptionally large clutches (6 eggs). In the clutch that was incubated for 34 days, at least 6 days elapsed between hatching of the first and the last chick. Clutch size had a significant influence on the length of the incubation period (ANOVA, clutches of 5 and 6 eggs pooled, $F_{3,278}$ = 3.885, P = 0.0096). Incubation periods of 5- and 6-egg-clutches differed significantly from the incubation

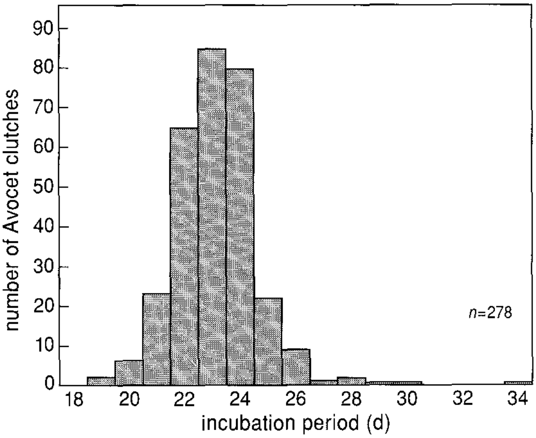

Fig. 1. Frequency distribution of lengths of incubation periods of 278 Avocet clutches.

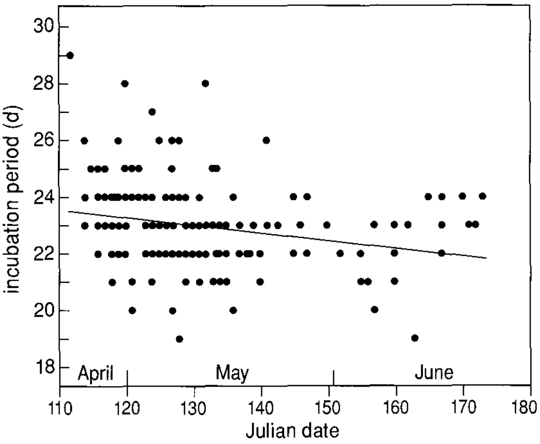

Fig. 2. Relationship between incubation period and the date of clutch initiation of Avocet 4-egg clutches ($y = -0.027x + 26.55$, $R^2 = 0.063$, $P < 0.001$, $n = 238$).

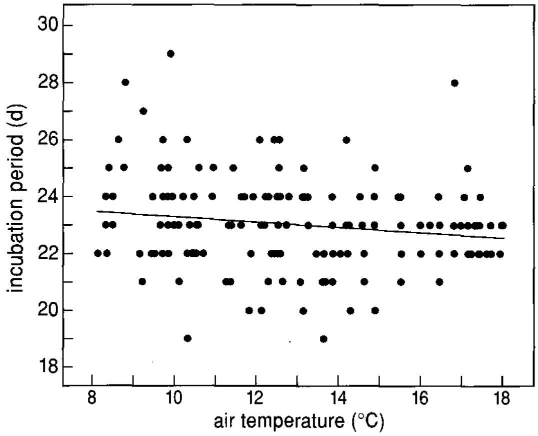

Fig. 3. Relationship between incubation period and the ambient incubation temperatures of Avocet 4-egg clutches ($y = -0.092x + 24.17$, $R^2 = 0.029$, $P = 0.008$, $n = 238$).

periods of 3-egg clutches (Tukey post-hoc test statistic 1.95, $P = 0.004$) and 4-egg clutches (Tukey post-hoc test statistic 2.18, $P < 0.001$). There were no significant differences among other clutch size classes. Clutches of more than four eggs contained eggs deposited by conspecific brood parasites (H. Hötker unpubl. data). In order to exclude possible effects of clutch size on incubation periods, all the following statistics are based on 4-egg clutches only.

Lengths of incubation tended to decrease in the course of the season. Incubation periods at the end of the breeding season in July were on average 1.7 days shorter than in the begining of the season in April (Fig. 2). The seasonal trends were consistent among all years with sufficient number of recorded incubation periods (1990, 1991, 1992, 1995, 1996). The regression coefficients for single years were, however, not statistically significant.

In all study years air temperature increased in the course of the breeding season. This increase in temperature could have been a reason for the decrease in the lengths of incubation periods, and, indeed, there was a weak but significant relationship between ambient incubation temperature and incubation period (Fig. 3) for the pooled data from all years. When the incubation periods were corrected for the temperature effect, the seasonal trends in all years were still apparent, and all regression coefficients (incubation period against date) remained negative. A stepwise multiple regression analysis of the pooled data set of all years with the time of clutch initiation and ambi-

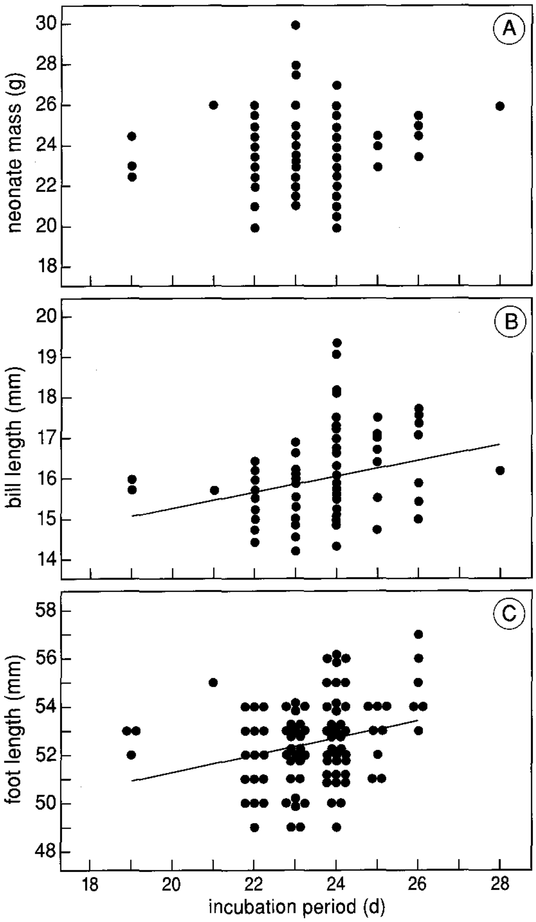

Fig. 4. Relationships between biometric measurements of neonate Avocets and incubation period; 4-egg clutches only. (A) Body mass ($R^2 = 0.005$, $P = 0.51$, $n = 95$), (B) Bill length (regression line: $y = 0.206x + 11.123$, $R^2 = 0.087$, $P = 0.003$, $n = 102$), (C) Foot length (regression line: $y = 0.370x + 43.893$, $R^2 = 0.076$, $P = 0.005$, $n = 101$).

Table 1. Survival of eggs and chicks of early and late broods (early brood: clutch initiation in the first half of the breeding season, i.e. before 20 May, fledging of chicks before 20 July; late brood: all other broods).

	Early broods	Late broods	Test statistic	$P <$
Daily egg survival	0.979	0.966	Johnson's test*, $z = 6.001$	0.001
Daily chick survival	0.949	0.936	$\chi^2 = 43.73$ $df = 1$	0.001

* Survival of clutches tested, because survival of eggs within a clutch can not be regarded to be statistically independent.

ent incubation temperature as independent variables, revealed a significant regression coefficient for the time of clutch initiation (regression coefficient $b = -0.0257$, $F = 14.465$, $P < 0.001$) but not for ambient incubation temperature ($b = -0.072$, $F = 1.424$, $P = 0.234$). Habitat (ANOVA, $F_{1,238} = 0.356$, $P = 0.551$), nest density of colonies ($F_{5,97} = 0.432$, $P = 0.825$), and the size of colonies ($r = 0.062$, $P = 0.464$, $n = 143$) had no effect on the length of the incubation period.

To assess how the length of the incubation period influenced the size of the hatchlings, univariate regressions with incubation period as independent variable were calculated. There was no significant relationship between incubation period and body mass of the neonate ($b = 0.087$, $F = 0.437$, $P = 0.510$; Fig. 4A). The regression coefficients for bill length and foot length were, however, significant (bill: $b = 0.206$, $F = 9.519$, $P = 0.003$; Fig. 4B; foot: $b = 0.370$, $F = 8.129$, $P = 0.005$; Fig. 4C).

To investigate possible causes of seasonal changes of incubation period, daily egg survival rates and daily chick survival rates in the first and in the second half of the season were calculated. Daily egg survival rates and daily chick survival rates were higher in the first half than in the second half of the breeding season (Table 1).

DISCUSSION

The arithmetic mean of 23.1 days for incubation periods found in this study corresponds to published data (Glutz von Blotzheim *et al.* 1977; Cramp & Simmons 1983). Cadbury *et al.* (in Glutz von Blotzheim *et al.* 1977) found a mean incubation period of 23.4 days for 230 clutches in England, and the data of 16 nests in Greece (Goutner 1985) give an average of 24.3 days (own calculation).

Avocet incubation periods were highly variable. Part of the variance could be explained by intraspecific nest parasitism. The incubation period, and thus the exposure time, of clutches produced by more than one female was longer than for one-female clutches. It is not known whether the increase in incubation period in multiple-female clutches was caused by less efficient incubation of the larger clutches or by a lack of synchronisation at hatching between the eggs of the host pair and the parasitic female. A less efficient warming of the eggs would support the incubation-ability hypothesis of clutch determination in waders (Anderson 1978; Kålås & Løfaldli 1987; Székely *et al.* 1994), which postulates that waders produce 4 (or 3)-egg clutches because they cannot efficiently incubate larger clutches. In any case, the longer exposure time which increased the mortality risk can be regarded as a cost of interspecific brood parasitism to the host pair.

The seasonal decline of the length of incubation periods meant that early clutches were exposed longer than late clutches. To demonstrate the effect on hatching success of a shortened incubation period, assume a constant daily survival rate of eggs throughout the season. With a daily egg survival rate of 0.971 (the mean rate for all eggs in the study; H. Hötker unpubl. data) according to Mayfield's formula (Mayfield 1961), the hatching probability of an egg rose from 0.475 in the beginning of the season to 0.500 in the end of the season. Changes in incubation period should thus be taken into account when calculating egg or nest survival rates. The rate of the seasonal decrease in incubation period in Avocets is roughly comparable to other published data. Murphy (1995) found a daily decrease of 0.05 days in Common Guillemots *Uria aalge*. Yogev *et al.* (1996) recorded values between 0.014 and 0.031 days for Spur-winged Plovers *Vanellus spinosus*.

It is unclear if ambient incubation temperature influenced incubation periods of Avocets. The data suggest that the seasonal reduction in incubation period was not primarily due to environmental conditions. Instead, Avocets seemed to follow a strategy of decreasing development time for late clutches. This would be advantageous since clutch mortality rates in Avocets increased towards the end of the season (Table 1). Moreover, the time for raising the chicks before the onset of postnuptial moult of adults was short for late hatching eggs. Moult and reproduction are generally regarded as conflicting processes (e.g. Svensson & Nilsson 1997) and, indeed, adult Avocets postponed primary moult for several weeks when they had late broods (H. Hötker unpubl. data). Murphy (1995) found a temperature-independent seasonal decrease in incubation period in Common Guillemots, interpreted as a mechanism to speed up development time well in advance of seasonal deterioration of environmental conditions.

How could Avocets decrease their incubation time? In principle adults could either increase their nest attentiveness or they could lay smaller eggs (Drent 1975). Neither nest attentiveness nor egg size have been measured in this study, so it is difficult to decide which tactic was followed by the Avocets. A decrease of incubation period over the breeding season could occur if Avocets delayed the start of incubation in early nests and/or started to incubate before having completed the clutch in late nests. This would make sense if incubation was more constrained by food availability early in the season than late in the season, and Avocets were forced to feed instead of incubating early in the season. Food availability in my study site seemed to increase throughout the breeding season. Avocets used a much higher proportion of time feeding in the beginning of the season in late April (up to 40% of daytime) than in late June (G. Kölsch pers. comm.; H. Hötker unpubl. data). However, there were no indications for changes in nest attentiveness in early versus late colonies. Observations from a distance revealed that the relationship between the numbers of 'Avocets sitting on the ground' and the number of clutches in the colony did not differ between the starting phases of early and late colonies (M. Berghorn & K. Küsters pers. comm.).

Mean egg size of many bird species is known to decrease in the course of the breeding season (e.g. Parsons 1972; Grønstøl 1997). If egg size had an effect on incubation period, a clear positive relationship between neonate mass and incubation period should be expected (Galbraith 1988; Grant 1991), but this was not found in this study. The regression in Fig. 4A, however, is based on raw data and does not take into account the water loss during incubation, estimated at 6.5 mg day^{-1} (Rahn & Ar 1984; data for mean fresh egg mass taken from Glutz von Blotzheim *et al.* 1977). Correcting for water loss would slightly increase the regression coefficient (Fig. 4A). Longer incubation periods being related to bigger eggs cannot, therefore, be excluded.

Independent of whether the prolonged incubation period in some clutches was caused by increased egg sizes, the gains in development that the neonates received per day of increased incubation period were relatively small (Fig. 4). The increase in bill length per additional incubation day was only 20% of the mean daily growth rate that chicks can expect in the field during the first 5 days of life (H. Hötker unpubl. data). In foot length this ratio was 43%.

Under these circumstances, were the longer incubation periods at the beginning of the season at all adaptive? Ydenberg (1989) explained nest departure times of Alcidae by trade-offs between different mortality and growth rates in the nest and at sea. Can the variations in incubation period of Avocets be explained by trade-offs between egg and chick mortality rates and embryonic and chick growth rates? A simple model may clarify the selective forces operating on incubation periods of Avocets. Assume that (1) the evolutionary currency involved in Avocet reproduction is only survival to fledging and not the energy reserves at fledging or the time of fledging, (2) the daily survival probability for eggs s_e is constant throughout the egg-phase, and the same is true for the survival probability s_c during the chick rearing period, (3) fledging occurs as soon as the chicks have reached a fixed body size z. This implies that increases in development due to longer incubation periods (bigger eggs) are directly transferred into a shorter chick rearing period. If (3a) during each extra day of incubation the body size of the neonate increases with a constant x, and (3b) the free ranging chick growth is y per day, then

$$z = z_0 + x \times ti + y \times tc$$

where z_0 is the initial size after the minimal incubation period, ti is the (extra) length of the incubation period (days), and tc is the length of the chick rearing period (days). Hence, the maximum length of the chick rearing period m is obtained by letting $ti = 0$ and thus $m = (z - z_0)/y$. The length of the chick rearing period can be written as $tc = m - a \times ti$, where $a = x/y$. Thus each extra day of incubation shortens the chick rearing period by a period a. The probability for an offspring to survive from egg laying to fledging may be written as follows:

$$s(ti) = s_e^{\,tl + ti} \times s_c^{\,(m - a \times ti)}$$

Simple arithmetic transformations gives

$$s(ti) = (s_e / s_c^{\,a})^{ti} \times s_e^{\,tl} \times s_c^{\,m}$$

The term after the first multiplication sign is a constant. $s(ti)$, therefore, increases with ti if $s_e / s_c^{\,a} > 1$. If this latter condition is fulfilled, prolonging incubation would be advantageous (but note that ti must always be smaller than m/a). If $s_e / s_c^{\,a} < 1$, incubation period should be compressed.

Do these relationships allow an interpretation of the seasonal decline in incubation periods? Additional data on the breeding biology of Avocets in the study sites (Table 1), help us to answer this question. Regarding the growth of the bill (a = 0.20, see above) there seemed to be no reason for prolonging incubation in the beginning of the season. Incubation should be as brief as possible at any time. The a-value of 0.43 for foot growth, however, indicated advantages of prolonged incubation in the beginning of the season and advantages of shorter incubation in the end of the season. There are hints that for young chicks foot growth is more important than bill growth. During adverse weather conditions bill growth but not foot growth is retarded (Hötker 1994). In the first days of the life of an Avocet, locomotion is the most important activity. The chicks have to run, often for several kilometres, from their breeding colonies to their feeding sites. For chicks running away is, besides hiding, the only means of escaping ground predators. The data on foot growth indicate that the length of incubation period might be determined by a trade-off between the rather slow but safe (in terms of daily mortality risk) development of the embryo in the egg, and the rather fast but risky development of the growing chick. With the possibility of influencing incubation periods (perhaps through egg size) birds possess a mechanism to adjust their reproductive investments to seasonally changing risks for eggs and chicks. That these mechanisms have not yet often been reported does not necessarily mean that they are not widespread. Seasonal variation in incubation period itself has been seldom addressed (Murphy 1995), and more studies in this field should be encouraged.

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SAMENVATTING

Welke factoren van invloed zijn op de broedduur van Kluten werd onderzocht aan de hand van 278 legsels van twee kolonies in het Duitse Waddengebied (Sleeswijk-Holstein). De broedduur (gedefinieerd als het aantal dagen tussen het leggen van het laatste ei van een legsel en het uitkomen van het laatste kuiken), varieerde tussen 19 en 34 dagen, en bedroeg gemiddeld 23.1 dagen. Er was een positief verband tussen legselgrootte en broedduur. Bij hele grote legsels (5 of 6 eieren, die waarschijnlijk waren gelegd door meerder vrouwtjes), liet de uitkomst het langst op zich wachten. Bij de meest voorkomende legselgrootte (van vier eieren) werd de broedduur korter naarmate het seizoen vorderde; er bestond een verschil van 1.7 dagen tussen de eerste en de laatste legsels. Dit seizoenspatroon kon niet worden verklaard uit veranderingen in de omgevingstemperatuur. Er werden ook geen relaties gevonden tussen broedduur en koloniegrootte, nestdichtheid en biotoop-kenmerken. Kluten die uit lang bebroede eieren kropen hadden langere snavels en grotere voeten. Vooral dat laatste lijkt van belang voor Kluten-kuikens als ze voor moeten rennen voor hun leven om aan grondpredatoren te ontkomen. Met behulp van een rekenmodel wordt uitgelegd hoe broedduur een compromis kan zijn tussen enerzijds de relatieve dagelijkse overlevingskansen van eieren en kuikens en anderzijds de relatieve groeisnelheden van embryo's (in het ei) en uitgekomen kuikens. (TP)

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