TIME BUDGETS AND BODY TEMPERATURES OF AMERICAN GOLDEN-PLOVER CHICKS IN RELATION TO AMBIENT TEMPERATURE

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Abstract. We studied time budgets of precocial chicks of American Golden-Plovers (*Pluvialis dominica*) on the tundra near Churchill, Manitoba, Canada, to assess how time budgets are influenced by environmental and body temperatures. Foraging time per day increased with increasing ambient temperatures and levels of solar radiation, as well as with age. This increase was due to an increase in the length of foraging bouts (i.e., the period of time in between two brooding bouts). The length of brooding bouts averaged 12 min, independent of ambient conditions or age. Body temperatures were lower under colder environmental conditions and increased as the chicks grew older. Based on measurements of cooling rates of penned chicks, we determined that at the end of a foraging bout, body temperature never fell below 35.5°C, which is high for a precocial chick. We suggest that in Churchill, American Golden-Plover chicks are not limited in their foraging time by ambient conditions, and they can collect sufficient food in the short periods of foraging that are available to them to sustain normal growth. By minimizing foraging bout length in favor of parental brooding, chicks may increase their digestive efficiency as well as save energy that would otherwise be expended on thermoregulation and locomotion.

Key words: behavioral thermoregulation, foraging ecology, Pluvialis dominica*, precocial, shorebirds, telemetry, time budget.*

Presupuesto de Tiempo y Temperaturas Corporales de Polluelos de *Pluvialis dominica* y su Relación con la Temperatura Ambiental

Resumen. Se estudió el presupuesto de tiempo de polluelos precociales de *Pluvialis dominica* en la tundra ubicada en las cercanías de Churchill, Manitoba, Canadá, para evaluar de qué manera el presupuesto de tiempo está influenciado por las temperaturas ambiental y corporal. El tiempo de forrajeo incrementó con el aumento de la temperatura ambiental, con los niveles de radiación solar y con la edad. Esto se debió a un incremento de la duración de las sesiones de forrajeo (es decir, el periodo de tiempo entre dos sesiones de empollamiento). La duración de las sesiones de empollamiento tuvo una media de 12 min, independientemente de las condiciones ambientales o de la edad. Las temperaturas corporales fueron inferiores bajo condiciones ambientales más frías, y aumentaron conforme a la edad de los polluelos. En base a medidas de la tasa de enfriamiento de pollos cautivos, es posible precisar que al final de una sesión de forrajeo, la temperatura corporal nunca es menor de 35.5°C, el cual es un valor elevado para un polluelo precocial. Sugerimos que en Churchill, el tiempo de forrajeo de los polluelos de *P. dominica* no está limitado por las condiciones ambientales y que los polluelos pueden acopiar suficiente alimento durante las cortas sesiones de forrajeo que disponen para mantener un crecimiento normal. La disminución de la duración de la sesión de forrajeo en favor de la incubación, les permite aumentar su eficacia digestiva y ahorrar energía, la que de otro modo podría emplearse en termorregulación o locomoción.

INTRODUCTION

The foraging behavior of precocial shorebird chicks is strongly affected by weather conditions. Young chicks forage by themselves, but as they are not yet homeothermic they lose body heat while foraging and must be brooded by their parents at regular intervals to be rewarmed. On the arctic tundra, where many shorebird species breed, the weather is often adverse, and this results in reduced time for the chicks to forage (Theberge and West 1973, Boggs et al. 1977, Beintema and Visser 1989). The way in which food availability and ambient temperatures together affect foraging time ultimately determines the northern limits of the breeding distribution. To understand this limitation, we need to understand how these factors determine foraging time.

Precocial chicks can remain mobile at reduced body temperatures (Norton 1973), which enables them to continue foraging while they are cooling. However, body temperatures below a certain threshold impair locomotion (Norton 1973, Myhre and Steen 1979, Pedersen and Steen 1979) and require that the chicks must be brooded. Accordingly, body temperature should affect foraging time, as suggested by Pedersen and Steen (1979) and Chappell (1980). Because a chick cools faster when the ambient temperature is lower (Visser and Ricklefs 1993), the body temperature threshold would be reached earlier under colder conditions, which would thus restrict the available foraging time. Other factors may also play a role in determining the available foraging time, apart from or interacting with the chick's body temperature. For example, digestive rate could limit the length of a foraging bout at the time a chick's stomach is filled. To date, we know little about the way in which physiology and behavior determine the foraging time available to a precocial chick. This study investigates the importance of body temperature in determining foraging time under fluctuating ambient conditions.

We studied the time budgets and body temperatures of both penned and free-living chicks of American Golden-Plovers (*Pluvialis dominica*) on the subarctic tundra near Churchill, Manitoba, Canada. Under varying weather conditions, we determined the total time available for foraging and assessed the length of foraging and brooding bouts as well as the body temperature at which chicks ended a foraging bout. These results were then compared to evaluate the importance of low body temperature, and its interaction with other factors such as age and environmental conditions, in determining the foraging time of shorebird chicks.

METHODS

STUDY AREA AND SUBJECTS

Observations and measurements were performed in 1997 and 1998 on the subarctic tundra near Churchill, Manitoba, Canada (58°45′N, 94°04′W). This location is at the southernmost border of the breeding range of the American Golden-Plover (Glutz von Blotzheim et al. 1971). In Churchill, American Golden-Plovers are common breeders (see also Jehl and Smith 1970) on hummocks and ridges with short, lichen-dominated vegetation (Byrkjedal and Thompson 1998). We observed a total of eight families with four chicks each and one family with three chicks. Average hatching date was 7 July, which is normal for the area (J. R. Jehl Jr., pers. comm.). Observations and collection of eggs were carried out under permit from the Canadian Wildlife Service (permit nos. WS-M44B and CWS98-M038a). Husbandry and laboratory procedures were approved by the Institutional Animal Care and Use Committee of the University of Missouri, St. Louis, Missouri.

ENVIRONMENTAL CONDITIONS

To correlate thermal properties of the environment with chick behavior, environmental temperatures were recorded continuously throughout the season. Two 3.5-cm spheres, one white and one black, with internally mounted thermocouples, were positioned 10 cm above ground in a microhabitat characteristic of foraging American Golden-Plover chicks. The white sphere measured ambient air temperature (T_a). The black sphere provided an approximation of the thermal environment with wind and solar radiation factored in, although not necessarily in the same fashion as experienced by the chick (Bakken et al. 1985, Walsberg and Weathers 1986). By subtracting the white sphere temperature from the black sphere temperature, we obtained a measure of radiative-convective load, independent of T_a. Levels thus obtained closely matched levels measured for comparison with a pyranometer (ANOVA: $F_{1,117} = 623.7$, $P <$

0.001, $r^2 = 0.84$; LI-200SA, Lincoln, Nebraska). Windspeed was measured 10 cm above the ground with a cup anemometer (A100L2, Grant Instruments Ltd., Barrington, UK), which was capable of measuring windspeeds ranging from 0 to 75 m sec^{-1}. The climate data were averaged over intervals of 15 min and recorded with a Squirrel 1204 data-logger (Grant Instruments Ltd.).

BEHAVIORAL OBSERVATIONS

Observations on the foraging behavior of free-living plover families were made from a blind or a vehicle at a distance of 100–200 m. Families occasionally moved toward the observer to distances as little as 5 m. To enable visual recognition, all chicks were marked individually within the family with red or yellow dye on the white down of the breast or circumcloacal region at the time when the chicks were caught.

Chicks were not always in sight. To be able to infer whether a chick was foraging or being brooded at these times, we used temperature-sensitive transmitters that were mounted externally on the backs of chicks. For this purpose all four chicks of a family were caught shortly after the fourth chick of the clutch hatched. At this time the chicks still return to the nest for brooding, and thus can be caught simultaneously. We caught the chicks by waiting from a distance until all four chicks were being brooded by the adult, and then running to the nest. The adult would fly off at our approach, but the chicks would hunker down at or close to the nest, where we would capture them. The procedure of measuring the chicks and attaching the transmitters took no more than 15 min, after which they were put back in the nest, and we left the area. The adult consequently returned to the nest within minutes. In each observed family, two chicks were equipped with a transmitter. When hatching order could be determined, we attached transmitters to the second and third chicks of the brood.

The behavior of the chicks was classified by combining visual observations with transmitter temperatures. This way, we could reliably monitor most brooding and foraging behavior of at least two chicks of a family, regardless of weather conditions or visibility. The two methods thus complemented each other and resulted in a good coverage of foraging behavior. When a chick carrying a transmitter started foraging, transmitter temperature dropped markedly, whereas at the start of a brooding bout it rose again. This process is depicted in Figure 1, for data between 05:00 and 09:00 and between 21:00 and 24:00. Brooding and foraging bouts could be determined precisely from these rapid changes in transmitter temperature, even when the chick was out of sight. During warm spells or when solar radiation was high, the transmitter heated up to such an extent during foraging bouts that it was impossible to conclude from transmitter temperature whether a chick was foraging or being brooded. Transmitter data were excluded when the ambient temperature was too high to determine the behavior of the chick with certainty, but since chicks were often more active at these higher temperatures, they could be followed well visually, and behavior could still be classified. This is shown in Figure 1 for the data recorded between 10:00 and 20:00. Since the chick could be seen foraging during this period, behavior could be classified as foraging.

Observations in 1997 were made 24 hr per day, which revealed that chicks did not forage between 23:00 and 03:00, while it was dark (Fig. 1, see Results). In 1998 observations were therefore restricted to daylight hours from 03:00 until 23:00. The nine broods were followed over a total of 45 days, making a total of 500 hr of observation time. Since a family could not always be found, or temporarily disappeared from sight or transmitter range, sample sizes differ per age and temperature class, and are given in the figure legends. The amount of observation time used to calculate foraging percentages was at least 1 hr but averaged 16.4 hr per age and temperature class. Behavior and transmitter temperature were recorded every 2 min for each chick and both parents when they were in sight. Chick behavior was categorized as either brooding or foraging; the latter including all nonbrooding behavior. Time budget analysis was based on all daytime observations. Analysis of the length of foraging and brooding bouts was based only on those bouts for which both start and end were known.

TEMPERATURE TRANSMITTERS

Temperature-sensitive transmitters were used only to differentiate between foraging and brooding behavior. Transmitters (type BD-2AT, Holohil Systems Ltd., Carp, Ontario, Canada) weighed 0.68 g (3.7% of neonatal body mass)
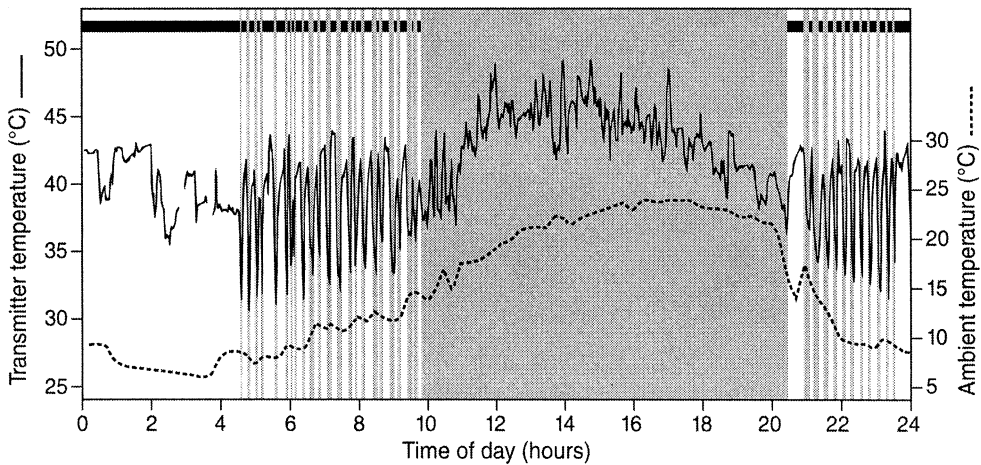
FIGURE 1. Example of transmitter temperature (solid line) of a 3-day-old American Golden-Plover chick throughout the day, indicating foraging and brooding behavior. Foraging bouts are shown as shaded vertical bars. Brooding (horizontal black bar) complements foraging. Ambient temperature is plotted as a dotted line. Between 23:30 and 04:30 no foraging occurred. From 04:30 to 10:00 and from 20:30 to 23:30 foraging and brooding bouts alternated. Between 10:00 and 20:30, high ambient temperatures rendered transmitter temperatures unreliable, but direct observation showed that chicks were foraging continuously during this period.

and were $13 \times 6 \times 3$ mm in size with a flexible antenna of 16 cm. They were attached with cyanoacrylate glue to the upper back of the chick just behind the neck. Transmitters remained in place for ca. two weeks. Chicks were not hindered by the transmitters. The added mass of the transmitter lies within the normal weight variation among chicks and for individual chicks throughout the day (Byrkjedal and Thompson 1998, KLK unpubl. data); thus the metabolic costs of carrying a radio are small. Chicks with transmitters grew normally, moved along naturally with the family, never got caught in vegetation, covered similar distances while foraging as chicks without transmitters, and showed no difference in bout lengths (GLM, residual analysis: no significant effect of carrying a transmitter on foraging bout length: $F_{1,968} = 2.6$, $P > 0.05$, $r^2 = 0.003$; or brooding bout length: $F_{1,897} = 2.3$, $P > 0.05$, $r^2 = 0.004$).

The temperature measured by the transmitter was intermediate between the temperature of the chick's skin and the air temperature, and thus did not measure body temperature. Each transmitter sent out a signal at a characteristic rate that could be picked up with a radio receiver carried by the observer. The signal rate was temperature dependent and was calibrated in a water bath against a mercury thermometer prior to attachment and when possible after retrieval. Signal

rate was determined manually by recording the time to receive 10 pulses. The signal could be received up to 500 m, but became faint when the chick moved behind a slope or a rock.

BODY TEMPERATURE

To measure body temperature (T_b) of chicks during foraging bouts, we hand reared seven chicks in 1998 from eggs collected in the field and hatched in an incubator. One day after hatching, the chicks were moved to an outside enclosure. The enclosure was circular with a diameter of 10 m, and surrounded by a chicken-wire fence 50 cm high, lined along the lower 20 cm with cloth and plastic, and fixed firmly to the ground with tent pegs to prevent escapes. A cover of large mesh netting kept out predators. An artificial brooder provided heat to the chicks. It consisted of a wooden box of 20 (height) $\times$ 30 (depth) $\times$ 20 (width) cm, with an entrance of 15 $\times$ 15 cm, in which a light bulb and a thermal blanket were placed, maintaining a temperature of up to 41°C closest to the light bulb. The light from the bulb served to direct the chicks to the brooder. Chicks learned to enter the brooder to be rewarmed within two days. From that day forward they were left in the enclosure continuously. Because naturally available food diminished rapidly in the enclosure, food and water were supplied daily. Food consisted of turkey

pre-starter mix (Puratone Corporation, Niverville, Manitoba, Canada), supplemented with a mix of tuna, chicken, oatmeal, and boiled eggs, as well as with freshly caught mosquitoes. Composition of the nutrients resembled natural insect food. Food was scattered on the ground to stimulate chicks to spend time foraging.

Foraging behavior was observed and T_b was measured from within the enclosure, where the observer sat quietly on the ground. A minimum of four and a maximum of eight individually color-banded chicks were followed simultaneously in the enclosure. Chicks were not disturbed by the presence of an observer, and often approached to catch mosquitoes that were attracted by the observer. Time budgets were determined by recording when the chicks entered and left the brooder. T_b was measured by quickly picking up the chick and inserting a greased, very thin thermocouple wire (30 gauge, tip dipped in a drop of nail polish to cover the sharp end), attached to a digital thermometer (Omega, Laval, Canada; accuracy 0.1°C) 1 cm into the cloaca. T_b was not measured more than once every half-hour in each chick, both during foraging and during brooding. After a T_b-measurement, behavior of the chick was not recorded for 5 min to allow the chick get back to its normal routine. Behavior of the chicks was not affected by the measurement. Chicks were released in a healthy condition in their natural environment at the end of the study, around their fledging age (22 days).

CALCULATION OF COOLING RATES

The availability of the artificially supplied food may have altered the behavior of the chicks, enabling them to stop feeding at a higher T_b than free-living chicks. Because of this, T_b measured in the enclosure could not be used to measure T_b at the end of a foraging bout. Instead, measurements of cooling rates and foraging bout lengths were combined to estimate this value. The cooling rates of chicks were calculated by subtracting the amount of heat lost through wet thermal conductance from the metabolic heat production of the chick (following eq. 5 in Visser and Ricklefs 1993). Metabolic measurements were taken from unpublished data of J. B. Williams and R. E. Ricklefs. Briefly, standard (SMR) and peak metabolic rates (PMR) of American Golden-Plover chicks of 1 to 20 days old were measured in a parallel laboratory study using an open-circuit respirometer. Temperature

was initially maintained within the thermoneutral zone to obtain an estimate of SMR and then was decreased by about 0.5°C per min until metabolism reached PMR and subsequently began to decrease. T_b and evaporation were monitored continuously throughout the trials. These measurements provided us with data for PMR and for the change in metabolic rate with the subsequent reduction in T_b, as well as with data for the wet thermal conductance, assuming a specific heat of 3.45 J g^{-1} °C^{-1} (Hart 1951). Using these detailed data on PMR and the changes in SMR with T_b, and knowing the foraging bout lengths, we could then, for each specific age and T_a, estimate the decrease in T_b of a chick during a period of time similar to the measured foraging bout length. Thus we obtained an estimate of the T_b at the end of a foraging bout for each age and T_a.

STATISTICAL ANALYSES

Data were analyzed using SPSS version 7.5 (SPSS Inc. 1997). Tests were performed as much as possible within a single model, using general linear models (GLM). Age, T_a, radiative-convective load, and wind were entered as covariates; time of day and nest as fixed factors. For each separate analysis, the statistics of the overall model are given, generally combined with the statistics for the individual covariates and factors. Foraging percentages were arcsine transformed prior to analysis, and percentages were calculated from the observations by grouping the data into classes of 5°C per age. Data on bout lengths were log transformed. Values reported are means, except for average bout lengths, where we calculated geometric rather than arithmetic means because the distributions of foraging and brooding bout lengths were strongly positively skewed.

RESULTS

ENVIRONMENTAL TEMPERATURES

Ambient temperatures in Churchill in July fluctuated widely (Fig. 2). The monthly averages were 18.7°C in 1997 and 15.0°C in 1998, which were considerably higher than the long-term average of 12.0°C (period from 1943–2000; source: Winnipeg Climate Centre, Winnipeg, Manitoba, Canada). For comparison, the summer of 1992 was much colder: the mean ambient temperature in July 1992 was 7.5°C, with an average maximum of 12.6°C and an average min-
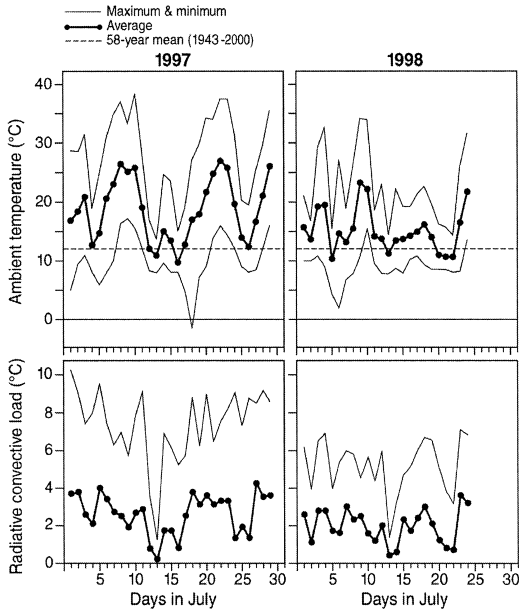
FIGURE 2. Ambient temperatures (upper panel) and levels of radiative convective load (indicating solar radiation; lower panel) in Churchill, Manitoba, Canada, in July 1997 and 1998. Daily averages (filled circles) are shown, as well as daily maxima and minima (thin lines). Mean ambient temperature from 1943 to 2000 was 12°C (dashed line).
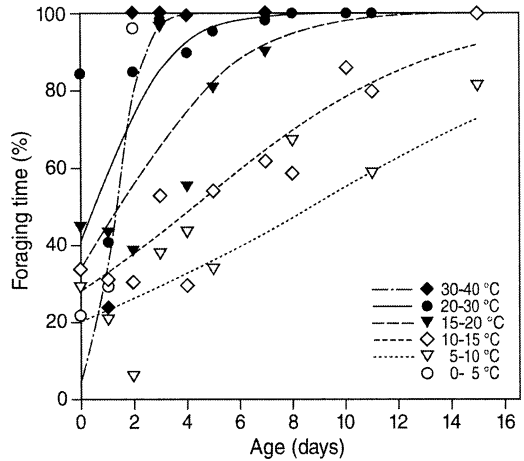

FIGURE 3. Time spent by free-living American Golden-Plover chicks on foraging and other activities resulting in body cooling, in relation to the age of the chicks and ambient temperature. Ambient temperature was grouped into six classes. Foraging time was calculated as a percentage of the active day (i.e., 03:00–23:00). Averages are based on 500 hr of observation time on nine families of golden-plovers, averaging 80 hr per day of age. Lines depict regressions for the upper five temperature classes, obtained by logistic regression.

imum of 2.3°C. The monthly minimum and maximum during our study were −1.4°C and 38.4°C respectively, both recorded in 1997. Like T_a, the radiative-convective load was higher in 1997.

TIME BUDGET

Foraging activity started at 03:00, just after first daylight (sunrise at ca. 03:30), and continued until dark at around 22:00 to 23:00, when the chicks spent an increasing amount of time brooding. From 23:00 onward, foraging activity ceased and transmitter temperature was continuously at brooding level, only occasionally dropping for a minute, likely due to a shift in position of either parent or chicks, or because parents switched brooding duties. Consequently, a maximum of 20 hr per day was available for foraging (03:00–23:00). Transmitter and ambient temperatures as well as the lengths of foraging and brooding bouts are plotted in Figure 1 as an example. Of the available 20 hr per day, the percentage of time that the chicks foraged increased with increasing T_a and with increasing

age of the chicks (Fig. 3; GLM: overall model: $F_{2,43} = 48.8$, $P < 0.001$, $r^2 = 0.69$; T_a: $F_{1,43} = 10.3$, $P < 0.01$; $T_a \times$ age interaction: $F_{1,43} = 54.4$, $P < 0.001$). The increase in foraging time with age was fitted with logistic regression for separate temperature classes (of 5°C or 10°C, see Fig. 3), giving significant fits ($P < 0.001$) for all classes except the coldest (0–5°C; Fig. 3). Pearson's r was 0.30, 0.29, 0.34, 0.38, and 0.44, respectively, for increasing temperature classes from 5–10°C to 30–40°C.

BOUT LENGTHS

Brooding bouts lasted 12 min on average during daytime (SD of geometric mean = −6/+13; range 2–302 min; $n = 899$), and did not vary with respect to age or environmental conditions. Foraging bouts (the period of time between two brooding bouts) lasted ca. 7 min in chicks up to 2 days old, but bout length increased rapidly as the chicks grew older and as T_a increased (Fig. 4). In addition to T_a, windspeed and radiative-convective load also significantly influenced the length of the foraging bouts, as did time of day (Table 1; $r^2 = 0.48$).
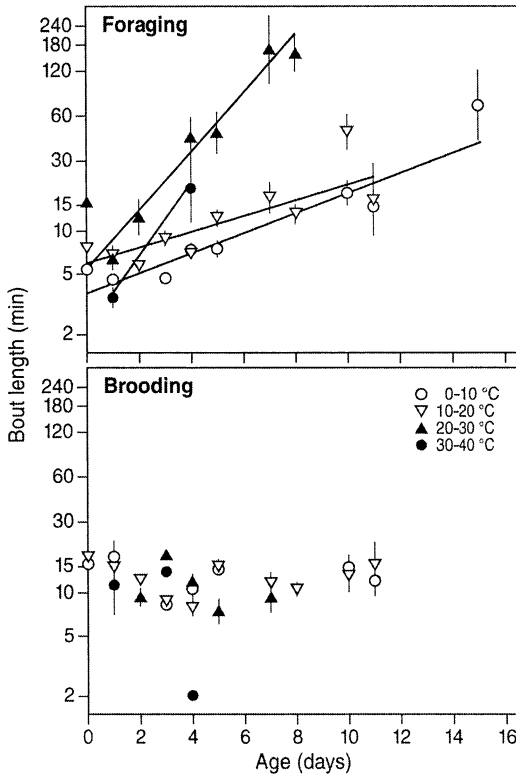
FIGURE 4. Mean length ± SE of foraging and brooding bouts in relation to age of American Golden-Plover chicks and ambient temperature, grouped into four classes. Symbols indicate geometric means. Lines depict significant linear regressions on log-transformed data. Sample size is 1002 foraging bouts and 899 brooding bouts (35 bouts per age per temperature class on average) recorded from nine families of golden-plovers.
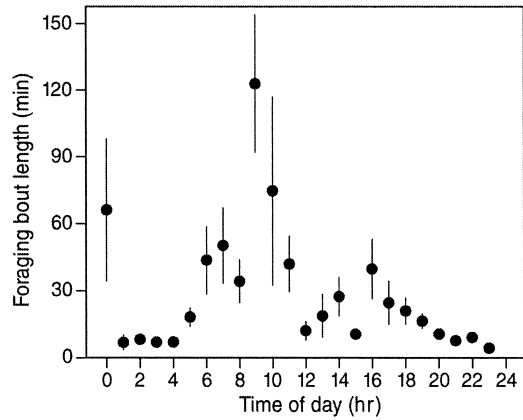

FIGURE 5. Mean length ± SE of American Golden-Plover chick foraging bouts in relation to the time of day. Data include nighttime observations. The longer foraging bouts at 00:00 reflect older chicks resting without being brooded, and do not reflect foraging, which does not occur at night in chicks. Sample size is 1054 bouts (44 bouts per age on average), recorded from nine families of golden-plovers.

Foraging bouts were considerably longer between 06:00 and 11:00 than during other parts of the day, and were shortest just after sunrise and before sunset (Fig. 5). The ratio between the foraging bout length observed and the foraging bout length predicted on the basis of age and T_a, had a very stable value of 1 to 2, except between 07:00 and 10:00, when it peaked to a maximum of 8. This indicates that bout length peaked during midmorning regardless of age and T_a. At night, chicks were brooded continuously up to 10 days of age, and consequently always showed a high transmitter temperature (Fig. 1). Chicks

TABLE 1. Factors affecting foraging bout length of American Golden-Plover chicks in Manitoba, Canada, 1997–1998, shown by the results of a general linear model on the logarithm of foraging bout length. ***$P < 0.001$.

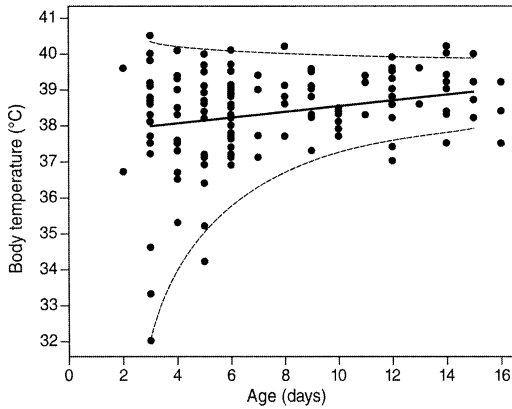| Source	Type III sum of squares	df	F
Model	109.4	33	26.9***
Intercept	13.4	1	108.8***
Age	17.5	1	142.1***
Radiative-convective load	5.3	1	42.9***
Windspeed	7.7	1	62.3***
Age × Radiative-convective load	13.4	1	108.7***
T_a × Radiative-convective load	12.7	1	12.7***
T_a × Windspeed	14.6	1	118.5***
Time of day	6.8	19	2.9***
Nest	6.3	8	6.4***
Error	119.3	968	

FIGURE 6. Body temperatures of American Golden-Plover chicks during foraging in an outdoor enclosure. Lines depict the regressions of minimum, maximum (dashed lines, fitted with inverse function) and mean (solid line; linear function) temperatures.
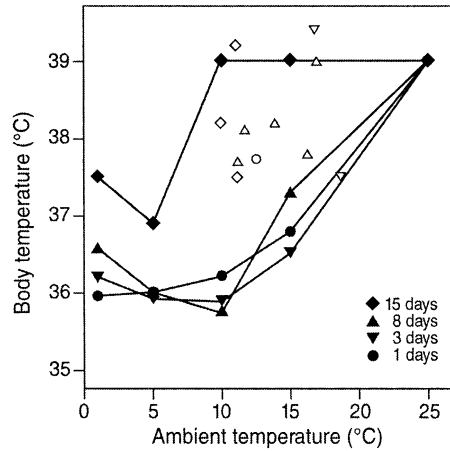

FIGURE 7. Body temperatures of American Golden-Plover chicks at the end of their foraging bouts, calculated from their cooling rates in relation to ambient temperatures. Each symbol represents the body temperature at the end of a foraging bout, for a specific ambient temperature (x-axis) and for a specific age (shaded symbols). Lines connect similar ages. As a comparison, unshaded symbols show the measured body temperatures of chicks at the end of a foraging bout in the enclosure; ages for these values are indicated by shapes as in the legend.

older than 10 days were not always fully covered by the parent because of their large size. Because of this, temperature of the transmitter would drop due to insufficient covering by the parent, giving the impression that the chick was foraging. In addition, by 15 days chicks were no longer brooded at night, but were seen lying close by the parent, which also resulted in lower transmitter temperatures. This is shown in Figure 5 as a longer foraging bout length at night, but reflects brooding and resting. The number of foraging and brooding bouts per hour ranged between 0.25 and 3 bouts per hr. The number of bouts increased with lower ambient temperatures, and decreased with age (GLM, number of foraging bouts versus age and T_a, overall model: $F_{2,10} = 15.2$, $P < 0.01$, $r^2 = 0.75$).

BODY TEMPERATURE

The T_b of chicks foraging in an outdoor enclosure varied widely (Fig. 6). The minimum T_b measured in the chicks was 32°C at 3 days of age. This minimum increased as the chicks grew older, and did not drop below 37°C after 6 days of age. Average T_b increased slightly with age (linear regression, $F_{1,144} = 10.2$, $P < 0.01$, $r^2 = 0.07$), and the range over which body temperature varied decreased until the chicks were 6 days old, after which it remained more or less stable. Body temperature was significantly higher when T_a was higher, even in chicks over 8 days old that already have a high degree of homeothermy. A higher radiative-convective load

increased the slope of this relationship, as did younger age (GLM, overall model: $F_{4,141} = 34.0$, $P < 0.001$, $r^2 = 0.49$; T_a: $F_{1,141} = 11.9$, $P < 0.01$; $T_a \times$ age interaction: $F_{1,141} = 67.3$, $P < 0.001$; $T_a \times$ radiative-convective load interaction: $F_{1,141} = 64.7$, $P < 0.001$; $T_a \times$ age $\times$ radiative-convective load interaction: $F_{1,141} = 48.3$, $P < 0.001$).

Body temperature at the end of a foraging bout was estimated by combining the calculated cooling rate of the chicks with the mean foraging bout length observed. Based on the calculations we found that T_b never dropped below 35°C, regardless of age or T_a (Fig. 7). In general, minimum T_b increased with warmer T_a and as the chicks grew older. However, chicks over 1 day old tended to let their T_b drop further when T_a was 5–10°C than when T_a was 1°C. The bout length used for calculating T_b was based on the regression between foraging bout length and age and T_a. Because this regression only estimates true bout length, the calculated T_b at the end of a foraging bout also only estimates the true T_b. For comparison, the T_b values measured at the end of a foraging bout in chicks foraging in the enclosure are also plotted in Figure 7, showing that actual minimum T_b in the enclosure was

equal to or higher than the calculated value of minimum T_b in chicks of 3 and 8 days old. Only in chicks of 15 days old did we find some minimum T_b values that were lower than the calculated T_b.

DISCUSSION

FORAGING TIME

Ambient temperatures in Churchill fluctuated considerably within a breeding season. Chicks experienced relatively warm summers in both 1997 and 1998. Our observations indicate that in 1997 and 1998, with an average T_a of 17°C, a 3-day-old American Golden-Plover chick in Churchill had 60–65% of the day available for feeding (excluding nighttime; calculation based on regression). At the more typical (58-year average) T_a for July (12°C), foraging time would decrease to ca. 40%. Given that American Golden-Plover chicks hatch at the beginning of July, and that they are particularly vulnerable to low T_a until they are ca. 10 days old, T_a during 1–20 July is most critical. During this period, the average T_a was below 10°C for eight days (40%) each year, on average, over the 58 years for which temperature recordings are available. This implies that during 40% of the time, a 3-day-old chick's foraging would be limited to less than 30% of the day.

The large fluctuation in T_a in Churchill is reflected in a similarly large fluctuation in available foraging time. On cold or windy days, growth of the chicks would be reduced or halted (Beintema and Visser 1989), which could result in death if the weather were unfavorable for several days in a row. Although ambient temperatures at Churchill generally provide enough foraging time for a plover chick, long spells of cold weather are not uncommon (e.g., 1992). Churchill is at the southernmost edge of the distribution of breeding American Golden-Plovers, and postnatal development is thus relatively unconstrained by climate. At higher and colder latitudes, less time is available for foraging. For example, on Southampton Island (64°N, 83°W) the average T_a in July is 9°C (Environment Canada, Ottawa, Ontario, Canada, unpubl. data), which corresponds to 30% of the active day available for foraging for a 3-day-old chick. At Barrow (71°N, 156°W), the northernmost breeding range of the plovers, the mean T_a in July is 4°C (data from the Alaska Climate Research Center, Fairbanks, AK), which reduces foraging time even further. Apparently even this small amount of time is enough for the chicks to fledge. Naturally, summer days are longer farther north, which partly balances loss of foraging time. However, whether a chick can fully use this longer day, or whether it forgoes foraging to sleep or because insects are less available during certain parts of the day, is not known.

Although T_a and age of the chick can largely explain foraging bout length, foraging bouts were exceptionally long during midmorning. At this time, T_a generally increased rapidly. After the cold nighttime and early-morning hours, chicks may use this increase in T_a, the associated reduction in thermoregulatory costs, and increased insect abundance (KLK, unpubl. data) to fill their stomachs.

AMBIENT TEMPERATURE AND BOUT LENGTH

In response to low T_a, American Golden-Plover chicks reduced the length of their foraging bouts and increased the number of bouts. Although T_a did have a strong effect on foraging time, the relatively moderate temperatures at Churchill do not appear to limit the foraging time of American Golden-Plover chicks. Our observations suggest this in a number of ways. First, instead of foraging for approximately the same length of time at a specific T_a, the lengths of foraging bouts varied widely, as shown by the low r^2 of the regression of foraging bout length with age and T_a. This indicates that environmental conditions are not the only determinant of the time activity budget of the chicks. Second, the increase in foraging bout length between 06:00 and 11:00 suggests that chicks were able to lengthen their foraging bouts when conditions other than T_a were favorable. If T_a were a limiting factor to the foraging time of the chicks, T_a would control bout length, and such an increase in bout length with time of day would not occur. Third, growth rate of the chicks in the field was as high or higher than that of chicks raised in the lab. Body masses of 16 chicks reaching ages over 3 days in the field were, with one exception, at or above the average mass of hand-raised chicks (van Gils and Krijgsveld, unpubl. data). Thus, foraging time apparently was sufficient for the chicks to satisfy their food requirements.

BODY TEMPERATURE AND BOUT LENGTH

Body temperature of the chicks in the enclosure fluctuated considerably. It increased as the chicks grew older, which is consistent with observations on other species (Bunni 1959, Pedersen and Steen 1979, Prinzinger et al. 1991), and decreased when the weather was colder. Minimum T_b at which a foraging bout ended also was lower on colder days. This corresponds roughly with the expectation that chicks cool faster when it is cold and consequently curtail foraging bouts, or cool further, or both. Although precocial chicks can lower their T_b considerably, low T_b involves such costs as reduced growth rate (Koskimies 1950, Rheinwald 1971, Beintema and Visser 1989). As the summer is short in northern regions, growth rate is important to a chick and thus may favor keeping T_b as high as possible. Secondly, when chicks become too cold, they lose their locomotory ability. Thus, T_b sets an upper limit to the length of a foraging bout (Pedersen and Steen 1979, Chappell 1980). However, minimum T_b measured in this study was high compared to the T_b of foraging precocial chicks in other studies. The T_b at the end of a foraging bout rarely dropped below 35.5°C, as shown by the T_b of the chicks in the enclosure as well as by the calculations of cooling rates of chicks. Several studies indicate that the T_b at which locomotion of precocial chicks becomes hampered lies well below 35.5°C (Norton 1973, Aulie 1979, Myhre and Steen 1979, Pedersen and Steen 1979, Gdowska et al. 1993). Thus, the T_b at which mobility starts to be hampered lies below the minimum T_b at which we found the chicks to cease foraging. It is therefore unlikely that T_b alone determines foraging bout length, although it may become more important when the weather is colder and cooling rates of the chicks are higher.

Minimum T_b was not fixed at one set point, but fluctuated with T_a and age. If low T_b were a proximate cause for the chicks to stop foraging, one would expect foraging to continue until T_b had reached a certain set point. The fact that it instead fluctuated with T_a further suggests that T_b alone does not determine foraging bout length. If bout lengths were constrained by an upper limit of, for example, body cooling, then the distribution of the data would be cut off beyond a certain maximum, resulting in a distribution with a strongly negative skew. However, data were strongly positively skewed. This again suggests that the chicks often return to be brooded before they have reached the maximum bout length permitted by body cooling.

OTHER DETERMINANTS OF BOUT LENGTH

We have shown that although T_b is an important factor in foraging behavior, it is not the main determinant of foraging bout length of American Golden-Plover chicks exposed to moderately low T_a. The rate of digestion may also contribute to ending a foraging bout. Insects are digested relatively slowly (Speakman 1987, Afik and Karasov 1995). If digestion generally lasts longer than a foraging bout, the stomach of the chick would be filled up after a certain time of foraging, forcing the chick to stop foraging. Since digestive efficiency is lower when T_b is lower (Kleiber and Dougherty 1934, Osbaldiston 1966), the rate and efficiency of digestion will increase when a chick is brooded and T_b is increasing. Because young chicks generally have a lower digestive efficiency than adults (Norton 1970, Karasov 1996), any behavior that increases digestive efficiency may play an important role in the foraging of shorebird chicks. In addition, the chick will save energy while digesting during brooding.

Another factor in ending a foraging bout is the balance between energetic costs and benefits of foraging. During a foraging bout, the chick cools down, which may suppress the chick's mobility and rate of food intake. Simultaneously, the metabolic rate of the chick increases (Williams and Ricklefs, unpubl. data). Thus, as the chick continues to forage, energy expenditure will at some point start to outweigh energy intake, at which time the chick should end its foraging bout. During foraging, the energy expenditure of a chick is high (Schekkerman and Visser 2001) and close to the maximum cold-induced and exercise-induced metabolism (Williams and Ricklefs, unpubl. data). Thus, by minimizing foraging time and increasing brooding time, a chick can considerably reduce its energy expenditure. Experimental work on the relationships between T_b, food intake, digestion, and energy expenditure under varying ambient conditions is needed to determine their roles in foraging behavior.

ACKNOWLEDGMENTS

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