THE EFFECT OF WEATHER ON TIME BUDGETS AND DEVELOPMENT OF CHICKS OF MEADOW BIRDS

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ABSTRACT Time budgets of chicks of the Lapwing, Black-tailed Godwit, and Redshank consist of alternating bouts of foraging freely, and being brooded by a parent. The lengths of brooding and foraging bouts depend on temperature and age. The foraging percentage, defined as percentage of time available for feeding, increases with the ambient temperature, as brooding bouts decrease in length, and foraging bouts increase in length. Foraging percentages also increase with age, when the chick improves its own thermoregulation. Above a threshold temperature brooding ceases. This threshold temperature decreases with age. Rain has an extra cooling effect, which cannot be expressed as a simple chilling factor, as the effect itself changes with age.From the data, a model has been derived, which can be used to predict the percentage of time available for feeding, based on the chick's age, and weather conditions. In adverse weather conditions, small chicks may need so much brooding, that too little time remains to feed. Chicks then show retarded growth, and may eventually die of starvation.

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INTRODUCTION

The Lapwing Vanellus vanellus, Black-tailed Godwit Limosa limosa, and Redshank Tringa totanus, are representatives of a bird community known as meadow birds in The Netherlands. They form an important and characteristic element of the Dutch avifauna (Van Dijk 1983, Piersma 1986). At present their numbers are declining because of the intensification of the agricultural management of their grassland habitat (Beintema 1983, 1986). The breeding biology of these species has been well studied (Van Balen 1959, Byrkjedal 1985, Grosskopf 1958, 1959, Klomp 1954, Lind 1961), but much remains to be learnt about the chick stage. In the chick stage most losses occur: while adult mortality ranges between 10% and 30% per year, and egg losses vary between 10% and 50% (Beintema & Müskens 1987), chick losses may exceed 75% (Beintema & Drost 1986). Causes of chick mortality include: lack of suitable food (insects), being killed by mowing, and adverse weather conditions for feeding. Food and feeding habits of chicks have been studied, but a relationship between food supply and mortality has not yet been established. The quantitative impact of mowing has not been estimated, but most observers suspect that losses among chicks, of at least the Black-tailed Godwit, are heavy. Weather is an important factor: in the Lapwing cold spells lead to retarded growth and increased mortality (Beintema 1978, Beintema & Visser 1989), in the Capercaillie Schröder *et al.* (1982) explain fluctuations at population level by weatherinduced chick mortality, and Koskimies & Lathi (1964) even consider cold tolerance in chicks as a key factor explaining northern and southern limits of the species' distributions.

In the present paper we investigate the effect of weather on the time budgets of chicks (feeding versus brooding bouts), and we present a descriptive model to predict the lengths of feeding and brooding bouts from the age of the chick, and the ambient temperature.

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METHODS

Study area and study design

The study was carried out in 1981 (Visser 1983) and 1984, in the meadow-bird reserve 'Kievitslanden' in Oostelijk Flevoland (52°24'N, 5°40'E). The reserve consists of 98 ha of wet grasslands, intersected at regular intervals by drainage channels. The reserve is heavily grazed by wild geese during the winter. The western part is mown in June, while the eastern part is grazed by cattle in summer. For details on management see De Jong (1972) and Zijlstra (1986).

The behaviour of meadow bird families with chicks was studied. As families wander considerably, and are susceptible to disturbance in their movements, a group of nests was fenced in, and a hide was erected just outside the enclosure, 2 m above the ground. Enclosures were 55-65 m wide, and 130-180 m long. They were constructed from wire-netting (mesh 1 cm), which was 50 cm high and firmly pinned to the ground. In order to minimize disturbance, construction work was limited to a daily maximum of three periods of one hour, during the middle of the day. The fence was completed within three days, in late April, before the first hatchlings appeared. Hatching dates were estimated with an 'incubometer', using flotation of the eggs (Van Paassen et al. 1984).

The wire-netting caused an unexpected problem: the adult birds sometimes took up a brooding posture just outside the fence, and called their chicks, which then tried to reach them in vain. Thus, one Godwit brood died of exposure. The problem was solved by attaching a 25 cm wide strip of black plastic foil to the fence, which made the chick invisible to a parent sitting on the other side. The fence did not deter the birds: additional pairs of Lapwing, Black-tailed Godwit, and Redshank started to nest within the enclosure. However, the set-up possibly repelled predators, as no eggs or chicks were lost to predation in either 1981 or 1984. In 1981, four pairs of Lapwings, four pairs of Blacktailed Godwits, and one pair of Redshanks nested within the enclosure. In 1984, there were four, two, and one pair(s), respectively. The chicks were never seen to favour the vicinity of the fence, where they may have profited from shelter or an improved microclimate.

Definition of terms

In the time budget of the chicks we simply distinguish between brooding bouts and foraging bouts. A brooding bout is an uninterrupted period of time spent being brooded by a parent. A foraging bout is the time spent between two brooding bouts. This time is not necessarily spent in continual foraging; in fact it is the 'time available for foraging'. However, smaller chicks do spend all of it foraging. Foraging and brooding bout lengths are not complementary (theoretically, a system with fixedlength brooding bouts and variable foraging bouts could exist). Therefore, brooding and foraging bouts are treated separately.

Observations

It was possible to observe the families in all corners of the enclosure from the hide. Observations were impaired by growing vegetation, and could not be continued beyond the first week of June. Observations began half an hour before sunrise and ended half an hour after sunset. The start of each brooding or foraging bout was registered. In all Lapwing and Redshank pairs, and in all Godwit pairs except one, the sex of the brooding parent could be distinguished by colour and size. One observer could monitor four families simultaneously.Total observation time was 687, 467, and 64 hours for the Lapwing, Black-tailed Godwit, and Redshank respectively. Seven Lapwing broods were followed, four of these being followed up until fledging. Six Black-tailed Godwit broods were followed, five up until fledging. One Redshank family was followed up until fledging. The other brood could not be observed in the tall grass, although the chicks were repeatedly captured. Chicks were ringed as soon as possible after hatching. Chicks were recaptured and weighed approximately every two days. Captures were done during the warm part of the day, and the procedure never lasted longer than 45 minutes. Usually it was possible to obtain 75% of all chicks during one round. Ambient temperature was recorded with a thermograph, in the vegetation at 'chick level', i.e. 10 cm above the ground. The registrations permitted readings up to every 2.5 minutes. Changes in the weather (cloudiness, rainfall) were noted.

Data analysis

The average air temperature was calculated for each brooding or foraging bout. Only fully observed, undisturbed bouts were used for analysis. The data were divided into two sets for each species: a 'dry' set without, and a 'wet' set with rain. The effect of the ambient temperature and the age of the chick on the length of brooding or foraging bouts was estimated in a regression model, for both the dry and wet data set.

RESULTS

Behaviour of parents and chicks

Most brooding was done by the female in the Lapwing and Black-tailed Godwit, while in the Redshank both sexes shared the duties (Table 1). In the Lapwing, the share of the male increased after two weeks, allowing the females to feed elsewhere. In the Black-tailed Godwit males were only seen brooding during the first week. In one case, when a family with small chicks was exposed to three cold, rainy days, the share of the male increased from 0% on the first day to 14% on the third. The chicks spent 24% of their time feeding during this day. The female spent all this time, and

Table 1. The share of the female (% of total brooding time by male and female) in brooding of the chicks, during the daylight hours.

Age	Lapwing	Black-tailed Godwit	Redshank	
days	(%)	(%)	(%)	
1- 7	96.8	94.4	50	
8-14	97.5	100		
8-10	-	-	50	
5-21	89.2	-	-	

all extra time when the male relieved her, feeding. In all species the initiative for brooding could be taken by the parent, or by the chicks. In the first case, a parent started to walk around the chicks, and took up brooding posture. In the second case chicks started calling, and walked towards the parent, which then took up a brooding posture.

Brooding was often done at the edge of a ditch, providing escape possibilities for the chicks, when disturbed by man or predator. Chicks were mostly brooded together. In one case, a Lapwing chick, when suddenly caught up in bad weather, failed to reach the brooding parent in time, and became immobile through hypothermia. The partner found the chick, and brooded it. Mortality on account of acute exposure was never observed. Brooding stopped when the chicks emerged to feed, or the parent got up and walked away. In the Lapwing and Black-tailed Godwit the female was mostly on guard when the chicks were foraging. The female left to feed elsewhere, when the male took over. In the Redshank both parents were often present.

Other animals (i.e. mammals, birds) were kept at least 20 m away from the chicks, and were chased by the male, and in severe cases of intrusion the female became involved in chasing as well. Mobbing a weasel attracted parents from a dozen other families of different species from throughout the area. Neighbouring families of the same species were often chased away, chicks being severely pecked. However, sometimes families tolerated each other, and allowed their chicks to mix. One Godwit chick permanently changed family, and was also brooded by the foster parent. Adoption has previously been observed in the Lapwing, under high density conditions (own data).

Growth and survival of chicks

Fig. 1 gives the growth curves for the chicks in the enclosures. Growth parameters are dealt with in the accompanying paper (Beintema & Visser 1989).In four Lapwing families followed until fledging, 4 of the 15 chicks died, at ages varying from 4 to 13 days. Three of these chicks showed retarded growth. All chicks fledged (16 in total) in five Godwit families followed up until fledging. This



Fig. 1. Development of the weights of chicks in the enclosure. For comparison with average growth in The Netherlands, lines give fitted Gompertz' growth curves, based on all available Dutch data (Beintema & Visser 1989). A = asymptotic value of Gompertz' curves.

is a remarkably high value since the average survival rate of Godwit chicks up until fledging has been estimated at 21% (Beintema & Drost 1986).One of the eight Redshank chicks died after 3 days. It did not differ in body weight from its surviving siblings.

The model

As the chicks grow, they require less brooding by their parents. A striking change in brooding behaviour was the increase in the period without any brooding during the middle of the day. A thres-



Fig. 2. Threshold temperature, above which no brooding by a parent takes place, as a function of age.

hold temperature was observed, above which there was no brooding. In Fig. 2 the highest temperature which brooding has ever been observed is given for each age (age given in days). Lines were fitted as

log(threshold) = C + a * age

C = 3.284, 3.142, and 3.159, a = -0.034, 0.071 and -0.101 for the Lapwing, Black-tailed Godwit, and Redshank, respectively. Below this threshold, brooding and foraging bouts alternated. This threshold decreased rapidly with age in the Godwit and Redshank, and decreased much more slowly in the

Lapwing.Below the threshold, the length of both brooding and foraging bouts varied with the ambient temperature. At lower temperatures, brooding bouts increased, and foraging bouts decreased in length. Bout lengths were fitted against ambient temperature, and the age of the chicks. A simple logarithmic model was assumed based on the supposed asymptotic nature of the relationship between both factors and the length of foraging or brooding bouts:

log(timespan) = constant + a * temperature + b * age

in which timespan stands for bout length (in decimal hours * 1000), temperature is given in °C and age in days. The model only serves to describe the data, not to explain it. In a more explanatory model, the temperature relative to the threshold would seem more appropriate, as a relevant parameter. However, the threshold was left out of the equation, because it would make the model very sensitive to the accuracy with which the threshold can be estimated, and it would introduce a strong interaction between the parameters.

The variation in the data was reduced (smoothed) by calculating two-dimensionally running mean bout lengths for each block of nine cells (three age values in days against three whole-degree temperature values), discarding means based on less than five observations. The model was fitted through the running means, for the three species, and for the dry and wet data set separately. Coefficients are given in Table 2. Residuals were calculated by subtracting the calculated fitted value (after smoothing) for the corresponding age and temperature from each observed value (before smoothing). The same model (timespan = residual) was fitted through these residuals, to estimate the mean deviation, for the positive and negative residuals separately.Foraging percentages were calculated for each combination of age and temperature from the fitted values for brooding and foraging bouts. The effect of rain was estimated by comparing foraging percentages for the dry and wet data set.

Simulation of foraging percentages

The model can be used to predict foraging percentages for chicks of various ages, under various weather conditions, using the coefficients from Table 2. This was done for our own data, to test the model. This looks like 'circular reasoning', as these data have been used to estimate the parameters in

Table 2. Coefficients in the model log(timespan) = C + A * temperature + B * age. BR is timespan = length of brooding bout, FO is timespan = length of foraging bout, DRY in dry weather, WET in rainy weather. Values for WET only applicable below 22°C for the Lapwing, and below 13°C for the Black-tailed Godwit. Timespan in decimal hours * 1000, temperature in °C, age in days. Age at birth defined as age 1, etc.

			A	В	С
Lapwing	DRY	BR	03985	00769	5.7035
	DRY	FO	.06002	.04014	3.9943
	WET	BR	081	.00655	6.1956
	WET	FO	.0517	.04328	3.7469
Black-tailed	DRY	BR	02889	11141	5.7498
Godwit	DRY	FO	.07178	.2263	3.7353
	WET	BR	0827	132	6.676
	WET	FO	.1784	.2363	2.6113
Redshank	DRY	BR	02214	0113	5.082
	DRY	FO	.1495	.1994	2.0476



Fig. 3. Relationship between observed and predicted foraging percentages.

the model. However, the true foraging percentages have not been used in the analysis, only the lengths of brooding and foraging bouts, which may vary independently, as has been pointed out earlier. The actual percentage of time available for foraging was calculated from the field observations, for each day for each family under observation. Predictions were made for the same days (only for the ages observed), using the formulae derived above, and the weather recordings of these days. The day was divided into periods of five minutes from sunrise to sunset. The foraging percentage was predicted for each period, during which the temperature was assumed to have been constant. These figures were then accumulated into a percentage for the day. Simulations were only performed for the Lapwing and Black-tailed Godwit. Fig. 3 shows the relationships between observed and calculated values. Lines fitted through the origin did not differ significantly from the line of equivalence, y = x (P < 0.01, F-test on sum of least squares).

Brooding and foraging bouts in dry weather

The relationships between bout length, age, and temperature are presented in Fig. 5 (brooding bouts) and 6 (foraging bouts). Fig. 4 demonstrates the three-dimensional relationship between timespan, age, and temperature, and how the twodimensional representation in Fig. 5 and 6 has been derived from this, giving the bottom plane with isorythms of timespan values, and two vertical cross sections. The effect of the ambient temperature on the time budget for small chicks did not differ much between the species. As the chicks grew older, the length of brooding bouts decreased, and the length of foraging bouts increased, at a given temperature. This change took place rapidly in the Black-tailed Godwit, but slowly in the Lapwing. Thus, in cold weather Lapwing chicks remain dependent on their parents much longer



Fig. 4. Three-dimensional diagram of the relationship age-temperature-timespan, illustrating composition of figs 4 and 5.



Fig. 5. Length of brooding bouts as a function of ambient temperature, and age of the chick. The diagram only shows the temperature range between the freezing point and the threshold temperature (Fig. 2). Diagonal lines connect points (age-temp. combinations) with equal bout lengths (decimal hours). No observations are available in shaded areas (values have been extrapolated here). Graphs give two sample sections through diagram, with mean deviation.



Fig. 6. Length of foraging bouts as a function of ambient temperature, and age of the chick. Explanation as Fig. 5.



Fig. 7. Foraging percentages in dry weather (7a), and rainy weather (7b), calculated with the coefficients from Table 2, as a function of ambient temperature, for four different relative ages. Values in shaded area are always 100%, because temperatures exceed threshold (Fig. 2). Data are insufficient to calculate separate threshold temperatures for rainy weather.

than Black-tailed Godwit chicks. In the Black-tailed Godwit, the lengths of brooding and foraging bouts greatly depend on age, and less on temperature, while in the Lapwing the reverse applies. The Redshank holds an intermediate position. To further visualize the different responses of the species, Fig. 7 has been constructed, using the coefficients from table 2. Fig. 7a shows the percentage of the time available for foraging, as a function of the ambient temperature, in dry weather, for four different relative ages, expressed as a percentage of the fledging age. Fledging age is 35, 27, and 26 days in the Lapwing, Black-tailed Godwit, and Redshank, respectively (own data). In cold weather (below 5°C) small chicks (1-3 days) of all three species, did not have more than 10 - 20% of their time available for foraging. At the same temperatures, half grown Black-tailed Godwits are virtually independent of brooding, half grown Redshanks can spend over 50% of their time feeding, and halfgrown Lapwings only 35%.

The effect of rain

For the 'wet data set', brooding bouts, foraging bouts, and foraging percentages were calculated. Rain has a chilling effect, because at the same temperatures brooding bouts tended to be longer, and foraging bouts shorter, than under dry conditions.In the Lapwing, brooding bouts did not increase in length at temperatures above 15°C, but were almost doubled at the freezing point, for all age classes. Foraging bouts were reduced by 25-45%, with little difference between age classes or temperatures. This resulted in a considerable reduction in foraging percentages (Fig. 7b). The effect of rain decreases with higher temperatures, and is only discernable when the temperature falls to below 22°C. The effect is rather independent of age.In the Black-tailed Godwit the effects of rain were about equally strong on brooding and foraging bouts. Brooding bouts could be doubled, and foraging bouts reduced to 50% at lower temperatures in small chicks. No reduction in foraging percentage was found at temperatures above 13°C. In this species there is a strong age effect: the chilling effect of rain diminishes with age.For the Red-



Fig 8. Relationship between growth (daily weight gain) and observed foraging percentages, in chicks of less than a week old.

shank, there are insufficient observations in rainy conditions to allow analysis. Values could only be calculated in the temperature range 7-9°C for ages 4-6 days.Within this range, reductions of foraging percentages of 29-57% were found. Within the same range, the reduction in foraging percentage varied from 20-47% in the Black-tailed Godwit, and from 28-35% in the Lapwing.The rain effect cannot be expressed as a simple 'chilling factor', analogous to usage in human Physiology (Leblanc 1975), as the effect itself changes with age.

Foraging percentages needed for growth

Weight increase per day was plotted against the foraging percentages observed in the field for the Lapwing and Black-tailed Godwit chicks, during their first week of life (Fig. 8). In both species, small chicks cannot maintain weight at foraging percentages below 25-30%. Growth is hampered at percentages below 50. The accompanying paper (Beintema & Visser 1989) shows how weight gain is related to the number of daylight hours above a certain temperature (15°C) in small chicks.

DISCUSSION

Development of thermal independence

As the surface area of birds is related to the twothird power of weight (Calder & King 1974), the ratio of heat production (mass related) to heat loss (surface related) in newborn chicks is most favourable in the Black-tailed Godwit (29 g at hatching),

and least favourable in the Redshank (16 g); the Lapwing (18 g) is intermediate. In spite of this, Redshank chicks forage at lower temperatures than Lapwing chicks and are almost as hardy as the much heavier Godwit chicks, indicating that Redshank chicks spend more energy on heat production than Lapwing chicks, or have better insulation. In addition to this, thermoregulation develops more slowly in the Lapwing. The Black-tailed Godwit and Redshank reach thermal independence at 40-50% of the fledging age, the Lapwing at 70%. In the Semipalmated Sandpiper, studied at Point Barrow, Alaska, brooding has been observed up until 65% of the fledging age (Ashkenazie & Safriel 1979), and in the Ringed Plover, studied in Greenland, until 75% (Pienkowski 1984). Wader chicks perform normal behaviour at body temperatures far below the adult's temperature, which reduces heat loss, and the cost of thermoregulation (Norton 1973, Ricklefs 1974, 1979, 1983). For example, small Lapwing chicks, when brooded, won't even let their temperature rise above 37.5°C (Myhre & Steen 1979), and let their temperature drop to almost 30°C when feeding (Visser, unpubl. data).

The role of the parents

Brooding of chicks may affect the time and energy budgets of the parents, as time spent brooding or standing guard cannot be used for foraging. Some weights of the Redshank parents are available up until 16 days after hatching (Visser unpubl. data), but no change could be detected in weights of either females or males during development of the chicks. When not on guard, parents often went feeding in other habitats to these that the chicks frequented. Ashkenazie & Safriel (1979) assumed that this avoids food competition between parents and chicks in arctic waders. This is not likely in our species as chicks and parents have different diets: chicks hunt for insects in the vegetation, while the adults probe for soil fauna. Later in the nesting season, the meadows may become a rather poor feeding habitat for adults, as the soil fauna retreats to greater depths, especially in well drained places (Visser 1982). When they have no chicks, the adults leave such areas, to gather in wetter places.

Zoogeographical aspects

Interspecific differences in cold tolerance have a zoogeographical and taxonomic perspective. Koskimies & Lahti (1964) have shown a relationship between cold-hardiness of ducklings, and the north-south extent of the species' distribution. They also found that chicks of gallinaceous birds are more sensitive to cold than those of ducks.Early development of thermoregulation in chicks has its costs. Energy intake has to be high, and problems of high metabolic rates in warm weather may even put a southern limit to the distribution of species (Koskimies & Lathi 1964). Less hardy chicks do not face these problems, but under cold conditions the time available for foraging is reduced, as the parents have to brood them. This does not prevent species with more sensitive chicks from penetrating far north. Koskimies & Lahti (1964) concluded that species with chicks of different cold-hardiness do not differ much in the northern limit of their distribution, but differ much more in their southern limit. They considered low energy-expending young as being ecologically more plastic, and generally more successful, with the Mallard Anas plathyrhynchos as a typical example within the duck family. The northern tetraonids have the more 'expensive', coldtolerant chicks among the gallinaceous birds. The chicks of the Capercaillie are more sensitive than those of the Black Grouse, Tetrao tetrix (Moss 1986), in spite of being bigger. Whether the Capercaillie is indeed a more southerly species than the Black Grouse by origin, cannot be judged from its present distribution, which has been severely restricted by man.

The three wader species in the present study range more widely from south to north than most other (more northern) wader species, which fits the ideas of Koskimies & Lathi (1964). Although the differences in range are small, the Lapwing is the least northern, the Black-tailed Godwit the least southern, and the Redshank embraces both regions. This is in accordance with the differences in their development of thermoregulation. There is an interesting difference between the Plover family (Charadriidae), to which the Lapwing belongs, and the Sandpipers (Scolopacidae), to which the Black-tailed Godwit and Redshank belong. Plovers have longer incubation periods, longer fledging periods, and longer total life spans than sandpipers (Beintema & Visser 1989), and the chicks depend on brooding far longer. Sandpipers have mostly northern distributions, in colder climates, whereas plovers occur all over the world, in many climates, with only few representatives in the arctic. One may suppose that not only weak thermoregulation, but also slow development is an adaptation to keep the running costs of chicks low. This may be less advantageous in cold areas than in arid habitats, where food is more likely to be scarce or thinly distributed at times. Latitudinal trends in growth rates have been shown by various authors (see Drent & Klaassen 1989). Slow development as a buffer against unpredictable food resources has also been postulated for a variety of seabird species (Drent & Daan 1980).

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SAMENVATTING

De tijdsbesteding van kuikens van drie weidevogelsoorten (kievit, grutto en tureluur) werd bestu-

deerd, in samenhang met de weersomstandigheden. De tijdsindeling van een kuiken bestaat uit een afwisseling van periodes waarin zij vrij lopen te fourageren en periodes waarin zij door een ouder worden opgewarmd. De lengte van opwarm- en fourageerperioden hangt af van de omgevingstemperatuur en de leeftijd van het kuiken. Het fourageerpercentage, ofwel het percentage van de tijd dat voor fourageren beschikbaar is, neemt toe bij stijgende temperatuur, omdat dan de opwarmperioden korter worden en de fourageerperioden langer. Het fourageerpercentage neemt ook toe met de leeftijd, omdat de eigen warmteregulatie van het kuiken zich beter ontwikkelt. Regen geeft een extra afkoelingseffect. Hiervoor kan niet met een eenvoudig 'behaaglijkheidscijfer' gecorrigeerd worden, omdat het effect zelf met de leeftijd verandert. Uit de gegevens is een model afgeleid waarmee fourageerpercentages voorspeld kunnen worden, als de leeftijd van het kuiken en de weersomstandigheden (temperatuur en neerslag) bekend zijn. Bij slecht weer kan het voorkomen dat kleine kuikens zoveel tijd nodig hebben om warm gehouden te worden, dat te weinig tijd overblijft om te fourageren. Kuikens lopen dan groeivertraging op en kunnen uiteindelijk van honger omkomen.