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Incubation pattern and foraging effort in the female Water Pipit *Anthus spinoletta*

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Incubation and foraging patterns of female Water Pipits *Anthus spinoletta* were studied in two breeding seasons in an Alpine valley of Switzerland. Decreased temperature reduced the length of periods spent off the nest (inattentive period), while decreased food availability led to a reduction in time spent incubating (attentiveness), shorter periods spent on the nest (attentive period), more frequent inattentive periods and higher foraging effort, measured as the product of frequency of inattentive periods and twice the flight distance to foraging sites. The negative relation between food availability and foraging effort resulted from more frequent foraging bouts and longer flight distances under poor food conditions. Feeding of the incubating female by the male did not affect foraging effort and attentiveness but did change the temporal pattern of inattentive periods from a few long to several short inattentive periods.

An incubation pattern must be scheduled to meet both the thermal requirements of the eggs and the energetic demands of the attending parent. In species where only one sex incubates, and thus must leave the nest from time to time to forage, birds have to balance these demands, especially under unfavourable temperature and food conditions. Energetic constraints caused by low food availability prolong foraging bouts and reduce the time spent in incubation (Drent *et al.* 1985, Moreno 1989, Smith *et al.* 1989), which results in suboptimal thermal conditions for the eggs (Johnson & Cowan 1974, Zann & Rossetto 1991, Williams 1993). At high air temperature there is a risk that unattended eggs will reach a lethal temperature (Zerba & Morton 1983a,b, Morton & Pereyra 1985). At low air temperature, unattended eggs cool more rapidly (Drent 1970, Caldwell & Cornwell 1975). The consequences of low egg temperature are slower development, sublethal teratogenic effects and even the immediate death of the embryo (Webb 1987). Thus, shorter and less frequent periods spent off the nest are advantageous for the developing embryos at both high and low temperatures. But higher attentiveness (time spent incubating the eggs) results in reduced foraging time and can increase the difficulty of the incubating parent to meet its own energy demand. As a consequence, the energy reserves of the attending parent will be reduced, with potentially negative effects on nestling care (Lifjeld & Slagsvold 1986). Moreover, there is increasing evidence, mainly from brood size manipulations, that high effort during reproduction can have negative consequences for future reproductive attempts and survival (Partridge 1989, Bryant 1991, Clutton-Brock 1991).

Single-sex incubating birds can minimize the conflict in balancing attentiveness and foraging, and thus reduce the proximate energy and ultimate fitness costs, by selecting a territory with high food availability or rich foraging sites nearby. In addition, energy budgets of incubating females can be ameliorated if nonincubating males feed their mates (nutritional hypothesis; Royama 1966). Lifjeld and Slagsvold (1989) and Smith *et al.* (1989) have shown that Pied Flycatcher *Ficedula hypoleuca* males increase their feeding rate when the nutritional state of the incubating female deteriorates.

In this paper we report the results of a study measuring the influence of air temperature, food availability and food provisioning by males on incubation pattern and foraging patterns of female Water Pipits *Anthus spinoletta.* In the Alps, Water Pipits breed above the tree line and start incubation in spring when mean daily air temperatures are below 10°C (C. Böhm, 1988, unpublished PhD thesis, University of Wien, C. Rauter, 1996, unpublished PhD thesis, University of Zürich). At that time of year, cold snaps and snow falls are not unlikely. Thus, the risk of chilling the unattended eggs is great, energy demand of the incubating female is high because of the high thermoregulatory costs at low temperature and arthropod food supply can change markedly. Based on the above outline, we tested the following predictions: (1) Attentiveness increases with decreasing air temperature. (2) Foraging effort of the female is negatively correlated with air temperature. (3) Females in territories with high food availability or with rich foraging sites nearby show higher attentiveness and a reduced foraging effort compared with females in territories with low food availability. (4) When the male feeds the incubating female more often, female attentiveness to the clutch increases and foraging effort decreases. Moreover, (5) feeding rate of the males should be negatively correlated with air temperature as well as food availability.

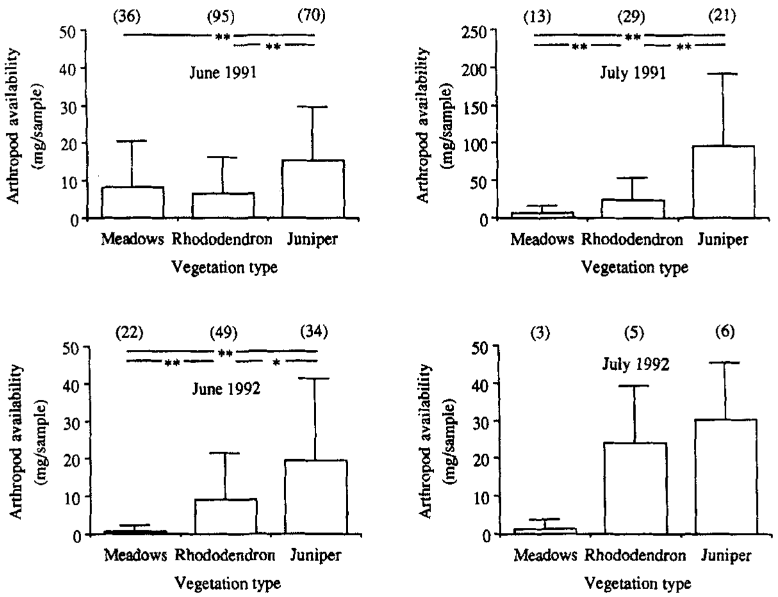

Figure 1. Arthropod availability, as assessed by 10 sweeps per sample (Brodmann *et al.* 1996), for each of the three vegetation types in which incubating female Water Pipits foraged mainly. The vegetation types corresponded to those of a vegetation map of the study area (Zumbühl & Burnand 1986). Data are given for the nestling period of the first (June 1991, June 1992) and second parts (July 1991, July 1992) of the breeding season. Vegetation types: Juniper, Rhododendron and meadows. Means and standard deviations are presented. Sample sizes are given in parentheses. Pairwise *t*-tests: $^{*}P < 0.05$, $^{**}P < 0.01$. Because of the small sample sizes, no pairwise tests were done for the second part of the breeding season 1992.

METHODS

Study area and birds

The study was carried out in the breeding seasons of 1991 and 1992 on a colour-ringed group of Water Pipits in the central Alps of eastern Switzerland near Davos in the "Dischma" valley, which runs from south southeast to north northwest. The 200-ha study area covered a cross section through the valley above the tree line between 1820 m and 2400 m. On the west-southwestern slope of the valley, the vegetation was mainly composed of Heather *Calluna vulgaris* and Juniper *Juniperus communis*. The east-northeastern slope was covered by Rhododendron *Rhododendron ferrugineum* bushes in the lower and middle parts and by lichen and trailing Azaleas *Loiseleura* in the upper part. The valley floor was characterized by meadows which were used to graze cattle and to make hay.

Water Pipits are small, insectivorous, ground-nesting passerines and are common in the Alps above tree line (Glutz von Blotzheim & Bauer 1985). At our study site, the birds arrived in April and nested in densities of up to eight pairs per 10 ha (K. Bollmann & A.R. Schläpfer, unpubl. data). Nests were built in late May or early June by the females underneath tussocks, inside clumps of vegetation or under the edge of a rock (C. Rauter, 1996, unpublished PhD thesis, University of Zürich). Incubation of the usual clutches of four or five eggs took about 15 days (K. Bollmann & A.R. Schläpfer, unpubl. data). Incubation was performed exclusively by the female, during which she was fed by the male (Pätzold 1984, C. Böhm, 1988, unpublished PhD thesis, University of Wien).

Ecological factors

The thermal environment of the eggs was assessed by mean daily air temperature rather than by direct temperature measurement in the nest cavity because the incubating females can react to disturbance by desertion. Mean daily air temperature is an adequate measure of the thermal environment of the nest. During the nestling period, a close correlation was found between mean daily air temperature measured in the nest (T_n) and that measured in the middle of the study area (T_a) by a weather station (Delta-T Devices Ltd, Cambridge, UK; $T_n = 3.6 + 0.9\ T_a$, $F_{1,71} = 228$, $P < 0.001$, $r^2 = 0.76$).

As a measure of food availability, we used the vegetation type at each female's main foraging site. The vegetation type was determined from a detailed vegetation map of the valley (Zumbühl & Burnand 1986). Females foraged mainly in Juniper (*Junipero-Arctostaphyletum*), Rhododendron (*Rhododendro-Vaccinietum*) and meadows (*Poion alpinae*). Measurements during the nestling period showed that arthropod availability differed significantly between these three vegetation types and increased from meadows through Rhododendron to Juniper (P.A. Brodmann & D. Bauer, unpubl. data; Fig. 1). To assess arthropod availability, the study area was subdivided into 50-m by 50-m squares, with each square corresponding to one vegetation type. In each square, ten sweeps with a net were taken, once in the first part (17–24 June) and once in the second part (14–21 July) of the breeding season. The collected arthropods were identified, dried and weighed (Brodmann *et al.* 1996).

Behavioural observations

Each nest was observed once during the incubation period. Behavioural observations lasted for at least 3 h (between 06.00 h and 10.30 h or between 16.00 h and 20.00 h) and were made from blinds, which were placed in such a way that the nest entrance as well as the foraging sites were visible.

The following variables were recorded. *Attentiveness* (min/h), total time which each female spent in the nest during an hour; *length of attentive periods* (min), mean duration of continuous spells in the nest; *frequency* (number/h) and *length* (min) *of inattentive periods*, the number per hour and mean duration of spells off the nest; *frequency of foraging bouts* (number/h), number of inattentive periods per hour during which the female foraged by herself; *flight distance to foraging site* (m), distance from the nest to the place where the female landed in the vegetation for foraging (the landing positions were marked on a map [scale 1:2500] of the study area). Usually, the female disappeared in the vegetation shortly after landing and foraging was assumed. This assumption seems reasonable, since foraging accounted for 60% of the time during 39 inattentive periods in which females were out of sight less than 10% of the time); *foraging effort* (m/h), product of number of foraging bouts per hour and twice the flight distance to the foraging site and *incubation feeding* (feedings/h), number of inattentive periods per hour where a male fed his female (this measure slightly underestimated the true number of feedings by males, because occasionally a female was fed two or three times during one inattentive period).

If an individual was observed in 1991 and 1992, one of these observations was randomly selected.

Data analyses

To control for effects of season and year, deviations from the seasonal means in each year, which refer to clutches hatched before 25 June compared with those hatched later, were used for all continuous variables in the correlation, regression and covariance analyses of incubation and foraging patterns and incubation feeding. To normalize data, the deviations of length of attentive periods, female foraging effort and flight distance were log-transformed.

Statistical analyses were performed with SAS (SAS Institute Inc. 1985) using the procedures CORR, REG and GLM. In the analyses of regression and covariance, Type II sum of squares were used. Stepwise analysis of covariance was done using the principles of the forward stepwise regression analysis (Dunn & Clark 1987).

RESULTS

Incubation and foraging pattern

Observations at 27 nests revealed the following incubation pattern. Mean attentiveness was 45.0 ± 5.2 (mean ± s.d.) min per h or 75.0% of the time. This percentage is near the high end of the 60–80% range reported for single-sex incubators (Skutch 1962, Haftorn 1978, Zerba & Morton 1983b, Weathers & Sullivan 1989). On average, attentive periods lasted 22.9 ± 11.9 min. Females left their nests 2.3 ± 0.7 times per h and stayed off the nest 6.6 ± 1.8 min each time. The length of the attentive periods and the frequency and length of inattentive periods, which determine attentiveness, showed the following correlations. The length of attentive periods and frequency of inattentive periods were strongly correlated ($r_{24} = -0.92$, $P < 0.001$), but neither of these two variables was related to length of inattentive periods. In a multiple regression analysis, 55% of the variance in attentiveness was explained by length of attentive periods, 45% by length of inattentive periods ($F_{2,23} = 144$, $P < 0.001$). Frequency of inattentive periods was not considered in this regression analysis because of its strong correlation with length of attentive periods and because it is more likely to be the consequence than the cause in this relationship. Frequency of foraging bouts and foraging flight distance, the two factors which determine female foraging effort, were positively correlated ($r_{24} = 0.46$, $P < 0.05$). Frequency of foraging bouts explained 13% of the variance in foraging effort and flight distance explained 41%. Foraging effort was negatively related to attentiveness ($r_{24} = -0.58$, $P < 0.01$). This relationship resulted from shortened attentive periods with increased foraging effort ($r_{24} = -0.72$, $P < 0.001$) rather than from longer inattentive periods at high foraging effort ($r_{24} = 0.004$, n.s.) and indicates that females employing a high foraging effort left the nest more frequently.

Males fed their female mates on average 0.7 ± 0.8 times per h. Eleven females were never observed to be fed despite at least 3 h of observation per female. The remaining 16 females received food from the males 0.3–2.6 times per h. Almost all of the feeding of females by males occurred in the vicinity of the nest. After being fed, the females either returned to the nest or flew off to foraging sites.

Factors influencing incubation pattern, foraging and incubation feeding

In the analyses of factors which influence the incubation pattern, foraging and incubation feeding, deviations from the seasonal mean in each year were used for each continuous variable to control for the effects of season and year. The deviations were then subjected to forward stepwise analysis of covariance. Results are summarized in Table 1 and Figure 2. Attentiveness was influenced only by the vegetation type at foraging sites, which explained 27% of the variance in attentiveness. Attentiveness was significantly higher in Juniper than in Rhododendron, where food availability was lower (Fig. 2a). When considering the individual components of attentiveness, we found females foraging in Juniper to have significantly longer attentive periods and to interrupt incubation significantly less often than females foraging in the other two vegetation types (Figs 2b and 2c). Inattentive periods were further influenced by incubation feeding: one extra feed to the female by the male increased the frequency of inattentive periods by 0.4 times per h (Fig. 2d) but shortened their duration by 1 min (Fig. 2f). Decreasing temperature lengthened inattentive periods by 0.4 min per °C (Fig. 2e).

Foraging effort was influenced by the vegetation type, as was attentiveness, but not by temperature and feeding by

Table 1. *Results of forward stepwise analyses of covariance on incubation and foraging patterns of female Water Pipits. Independent variables were mean daily air temperature, vegetation type at foraging site and male incubation feeding rate. Effects of season and year were controlled for by using deviations of seasonal means of each year for the analyses. Seasonal means refer to clutches hatched before 25 June compared with those hatched later. Deviations in length of attentive periods, foraging effort and flight distance were log-transformed. Independent variables are listed if they were significant predictors of the dependent variable at the* P < 0.05 *level. Var: variance explained, b: slope of continuous variables*

Incubation pattern					
Model	d.f.	*F*	P	b	Var (%)
Attentiveness					
Vegetation type	2,23	4.4	<0.05	—	26.9
Length of attentive periods					
Vegetation type	2,23	7.1	<0.01	—	37.0
Frequency of inattentive periods					
Vegetation type	2,22	8.0	<0.01	—	28.9
Incubation feeding	1,22	9.5	<0.01	0.4	17.0
Overall	3,22	10.9	<0.001		58.7
Length of inattentive periods					
Air temperature	1,23	14.6	<0.001	0.4	27.1
Incubation feeding	1,23	11.8	<0.01	−1.1	21.8
Overall	2,23	14.9	<0.001		55.4

Foraging pattern					
Model	d.f.	*F*	P	b	Var (%)
Foraging effort					
Vegetation type	2,23	4.7	<0.05	—	28.2
Frequency of foraging bouts					
Vegetation type	2,23	4.1	<0.05	—	25.5
Flight distance					
Vegetation type	2,23	4.0	<0.05	—	24.8

the male. Females foraging in Juniper showed a significantly lower foraging effort than females foraging in meadows (Fig. 2g) because of the significantly fewer foraging bouts and shorter flight distances (Figs 2h and 2i). Each of the factors which showed an effect on female behaviour explained between 17% and 37% of the variance in the corresponding behaviour (Table 1).

Incubation feeding activity by the male was not affected by any of the ecological factors. Neither air temperature nor vegetation type was a significant predictor of incubation feeding.

DISCUSSION

The data confirmed only one of the five predictions presented in the introduction to this paper. With increased food availability, attentiveness increased and foraging effort decreased (prediction 3). Positive relationships between food availability and attentiveness have also been reported for the single-sex incubating Pied Flycatcher (Smith *et al.* 1989) and Wheatear *Oenanthe oenanthe* (Moreno 1989), but female Wheatears shortened the inattentive periods and kept the attentive periods constant as food increased, whereas female Water Pipits kept inattentive periods constant and prolonged attentive periods. The decreased foraging effort from meadows through Rhododendron to Juniper resulted from a corresponding decrease in number of foraging bouts and flight distance (Figs 2h and 2i). The negative relationship between flight distance and food availability may be the consequence of a faster food depletion at low food availability compared with high food availability. Theoretical considerations (Andersson 1978, 1981, Houston *et al.* 1985) suggest that birds should forage closer to the nest on a territory where food availability is high, since food around the nest is not as rapidly depleted or is renewed more quickly compared with a territory with low food availability.

In all other respects, the results deviated from the predictions. Decreased air temperature increased neither the foraging effort (prediction 2) nor the attentiveness (prediction 1), although it shortened the length of the inattentive periods. These findings, which are in contrast to those of some other studies (Haftorn 1979, Davis *et al.* 1984, Drent *et al.* 1985, Smith & Montgomerie 1992), are unlikely to have been caused by the method used to quantify the variables. When absolute values rather than deviations from the seasonal means of each year were used in the analyses, results did not change. The lack of a temperature influence on attentiveness, despite the positive correlation between temperature and length of inattentive periods, probably resulted from the fact that in our study variance in the length of inattentive periods was small and explained less of the variance in attentiveness than did length of attentive periods, which was not related to temperature. A possible biological reason was the unusually favourable weather conditions in both years of the study. Air temperatures in June and July were on average 0.9°C higher than the 10-year mean (K. Bollmann, 1996, unpublished PhD

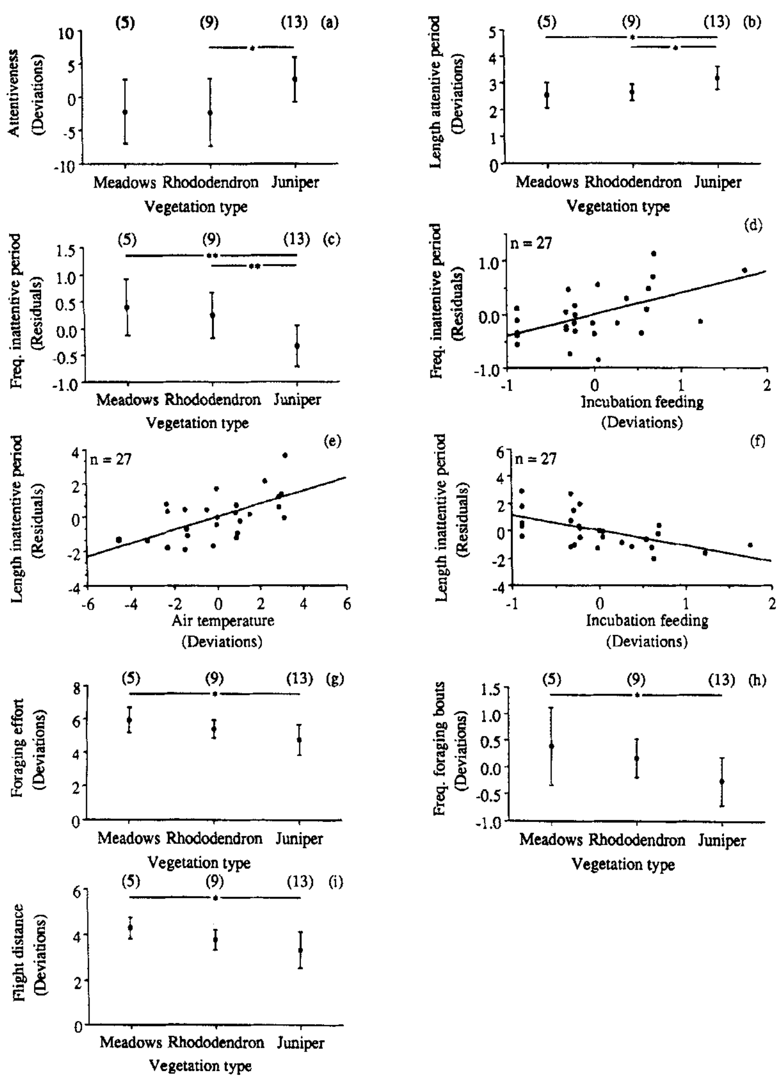

Figure 2. Incubation and foraging patterns of female Water Pipits (y-axes) in relation to air temperature, vegetation type at foraging site or incubation feeding by their males (x-axes). Effects of season and year were controlled for by using deviations of seasonal means of each year for the analyses. Seasonal means refer to clutches hatched before 25 June *v* those hatched later. Deviations in length of attentive periods, female foraging effort and flight distance were log-transformed. The y-values of frequency and length of inattentive periods are given as residuals after removing the effect of the variable (see Table 1) which was not used as x-variable in the plot. (a) Attentiveness in relation to vegetation type; (b) Length of attentive periods in relation to vegetation type; (c, d) Frequency of inattentive periods in relation to vegetation type and incubation feeding; (e, f) Length of inattentive periods in relation to air temperature and incubation feeding; (g–i) Foraging effort, frequency of foraging bouts and flight distance in relation to vegetation type. Means and standard deviations are presented for each vegetation type. Sample sizes are given by parentheses. Pairwise tests were done using the Scheffé method (Sokal & Rohlf 1981): * $P < 0.05$, ** $P < 0.01$.

thesis, University of Zürich). The resulting mean daily air temperatures (range 5.0–15.7°C) may not have been low enough to endanger embryo survival under the observed frequency of inattentive periods and also may have improved the food supply, thus masking temperature effects on attentiveness and foraging effort that might have been observed in less favourable years.

The absence of an effect of incubation feeding on female attentiveness and foraging patterns, which contradicts prediction 4, may have arisen from the low rate at which males fed their mates. Mean frequency of incubation feeding (0.7 feedings/h) in male Water Pipits was much lower than frequencies (1.6–4.7 feedings/h) reported in studies of other species, which found positive effects of incubation feeding on female attentiveness (Lifjeld *et al.* 1987, Moreno & Carlson 1989, Halupka 1994). Incubation feeding changed the temporal pattern of inattentiveness from a few long to several short bouts (Figs 2d and 2f). When females use several short inattentive periods, egg temperature will cool less during each inattentive period than when they use few long inattentive periods. Thus, the mean egg temperature will be higher and the variance lower. These temperature conditions enhance egg development and thus shorten the length of the incubation period (Webb 1987).

The low feeding rates of the males and the absence of any influence of ecological factors on these rates, contradicting prediction 5, indicate that incubating females were not severely energy limited in these two, probably benign, years. This conclusion is further supported by a high hatching success of eggs (87%, n = 398 nests; K. Bollmann & A.R. Schläpfer, unpubl. data) and by the lack of a negative correlation between female behaviour during incubation and female parental care for nestlings (C. Rauter, 1996, unpublished PhD thesis, University of Zürich).

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