

REPRODUCTIVE SUCCESS OF WATER PIPITS IN AN ALPINE ENVIRONMENT

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Abstract. To understand the evolution of avian reproductive strategies it is important to assess how differences in reproductive success are related to timing of the breeding season, quality of nesting territories or breeders, or to a combination of these factors. Over three years, we studied the reproductive performance of female Water Pipits (*Anthus spinoletta*) in a temporally and spatially variable alpine environment. The study area covered two valley slopes that differed in the probability of nest predation, food availability, and climate. Nest predation and harsh weather were the main proximate causes of differences in female reproductive success. Because these two environmental factors were locally unpredictable, individual females could best optimize their seasonal reproductive success by choosing the “right” breeding time. The average number of young fledged per season was inversely related to the date of initial breeding and increased from females with only first attempts, through females with replacement clutches, to females that raised two broods. Hence, the main advantage of early breeding lies in the chance of rearing a second brood after the first has fledged, or of producing a replacement clutch if the first fails due to predation or harsh weather.

Key words: *Anthus spinoletta*, breeding area, predation, reproductive success, time of breeding, variable environment, weather conditions.

Éxito Reproductivo de *Anthus spinoletta* en un Ambiente Alpino

Resumen. Para entender la evolución de las estrategias reproductivas de las aves es importante determinar cómo las diferencias en el éxito reproductivo se relacionan con el comienzo de la época reproductiva, la calidad de los territorios de nidificación o los reproductores o con una combinación de estos factores. Durante un período de tres años, estudiamos el desempeño reproductivo de hembras de *Anthus spinoletta* en un ambiente alpino temporal y espacialmente variable. El sitio de estudio comprendió dos laderas que diferían en la probabilidad de depredación de nidos, disponibilidad de alimento y clima. La depredación de nidos y el clima severo fueron las principales causas proximales de la diferencia del éxito reproductivo de las hembras. Debido a que ambos factores ambientales fueron localmente impredecibles, cada individuo hembra podía optimizar el éxito de su período reproductivo eligiendo el tiempo “correcto” para reproducirse en la temporada. El número promedio de juveniles por temporada se relacionó inversamente con la fecha del inicio de la reproducción y aumentó desde hembras con sólo un intento de cría, pasando por hembras que reemplazaron sus nidadas, hasta hembras que criaron dos nidadas. Por tanto, la ventaja principal de reproducirse tempranamente en la temporada está dada por la posibilidad de criar una segunda nidada luego de la partida de los primeros juveniles o de producir una nueva nidada si la primera falla debido a depredación o clima severo.

INTRODUCTION

Reproductive success depends on both the number of young in a brood and the number of broods raised per season (Hötter and Sudfeldt 1982, Askenmo and Unger 1986, Westmoreland et al. 1986). There is, however, a trade-off between these two fitness components whenever

the amount of investment in one brood affects the probability or success of subsequent broods within or between years (Nur 1990). The optimal solution of this trade-off for a potentially multi-brooded bird will vary with individual qualities, ecological conditions, and other factors that influence survival and reproduction of adults and young (Stearns 1992).

Ground-nesting birds breeding in alpine environments offer an excellent opportunity to study how environmental conditions affect reproductive tactics and success. The short alpine breeding season constrains possibilities for second broods, and the characteristic high temporal

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and spatial variability in weather, food availability, and predation are important determinants of breeding success (Ricklefs 1969, Yom-Tov 1974, Martin 1992). Extensive rainfalls and snowstorms in summer can result in partial or complete nest failure (Verbeek 1970, Hendricks and Norment 1992, Bollmann et al. 1997). Climatic conditions vary, however, with altitude and season, and they differ among years and slopes (Franz 1979). This causes spatial and temporal variation in vegetation types and snow-melt patterns, which translate into differences in types and numbers of predators and food items (Neumeyer 1984, Bauer 1992). Some of these differences are fairly permanent (e.g., vegetation in relation to altitude and slope) but others, like the amount of food and the probability of predation, are less predictable. While the effects of a temporally and spatially variable food supply on settlement strategies and breeding success have been investigated in several bird species, in comparison the role of nest predation is poorly understood. Although predation can have a considerable impact on the fitness of passerines (Dunn 1977, Bollmann et al. 1997, Sorace et al. 2000), predators are often excluded from analyses of individual reproductive performance, probably because they are rarely observed in action and, hence, remain unidentified.

In this study, we investigate the impact of breeding period, nest predation, weather conditions, and microclimate on fitness parameters in an alpine population of individually banded Water Pipits (*Anthus spinoletta*), studied over three years on opposite slopes of a valley. We first analyzed reproductive differences in space and time. Second, we compared ecological and demographic differences between slopes, years, and breeding periods. Third, we investigated factors causing temporal and spatial differences in reproductive success.

METHODS

STUDY AREA AND STUDY SPECIES

The study was carried out during 1990, 1991, and 1992 in the central Alps of eastern Switzerland in the valley of Dischma (46°6'N, 9°53'E) near Davos. The 260-ha study area covers a cross-section through the valley above treeline, between 1820 and 2300 m above sea level. The valley bottom runs from southeast to northwest and is dominated by meadows and pastures. The vege-

tation of the valley sides, with slopes up to 50°, is dominated by dwarf shrubs and alpine pastures. On the southwestern slope the vegetation is mainly composed of heather (*Calluna vulgaris*) and juniper (*Juniperus communis*). The northeastern slope is covered by rhododendron bushes (*Rhododendron ferrugineum*) in the lower and middle parts and by lichen and trailing azaleas (*Loiseleuria procumbens*) in the upper part.

Meteorological data were taken from the federal stations in Davos-Dorf (1590 m) and Weissfluhjoch (2690 m). These two stations are 8.8 and 12.5 km, respectively, from the study area and at a mean altitude of 2140 m. Measurements at the two stations thus can be assumed to represent climatic conditions in the study area adequately. Air temperature was recorded from Davos-Dorf and was corrected by -0.62°C per 100 m altitude. From 1990 to 1992 mean temperatures for January, July, and the whole year were -6.7°C , 10.4°C , and 1.1°C , respectively; all were higher than the long-term averages (Bollmann 1996). During the same three years annual precipitation averaged 1213 mm. For May, the month of mating, nest construction, and egg laying, average air temperature was 5.6°C in 1990, 0.2°C in 1991 and 5.6°C in 1992. For precipitation the respective values were 74.1 mm, 91.1 mm, and 54.1 mm, and the amount of new snow was 7.5 cm, 72.5 cm, and 5.0 cm. In all summer months there is a chance of snowfall, with snow cover persisting up to 3 days.

Water Pipits are small, insectivorous, ground-nesting passerines, and are common in the Alps above treeline (Glutz von Blotzheim and Bauer 1985). In spring, males arrive before females and settle in accordance with snow cover (Bollmann et al. 1997). In our study area, densities ranged from 3.5 to 7.8 territories per ha, depending on slope and year (Bollmann and Reyer 1999, A. R. Schläpfer unpubl. data). Water Pipits feed on arthropods which they collect both within their breeding territories and at communal feeding sites (Frey-Roos et al. 1995, Bollmann et al. 1997, Brodmann et al. 1997). Nests are exclusively built by the female underneath tussocks, inside clumps of vegetation, or under the edges of rocks (Pätzold 1984, Böhm and Landmann 1995, Rauter and Reyer 1997), and eggs are incubated for 15 days (Bollmann 1996). Further details on nest site characteristics, territory quality, foraging behavior, and reproduction are given by Reyer et al. (1997), Brodmann and

Reyer (1999), Rauter and Reyser (2000) and Rauter et al. (2000, 2002).

FIELD METHODS

Each year, observations started between 22 April and 1 May, about the time the first individuals arrived. Adult birds were captured with mist nets either during the migration into the valley or at nests. Each bird was measured, weighed, sexed, and individually color-banded. In cases where sex determination by the absence or presence of a brood patch or via morphological data was not possible, behavioral observations were used to establish sex. Because some birds had been born before 1990, minimum ages are used in the analyses.

Territory mapping and nest finding. Regular observations of territorial, feeding, and reproductive behavior were done every 2 to 4 days throughout the breeding season. Locations of nests and birds tending them were recorded on a map (scale 1:25 000); territory size and shape was determined by the minimum concave polygon method (Clutton-Brock et al. 1982). Nests were marked by a 50–60 cm bamboo stick placed 2 m from the nest entrance. This stick allowed us to quickly find the nests without increasing predation risk by marking them directly. We monitored nests daily when hatching or fledging was expected. In this way the causes of nestling mortality could be ascertained in most cases. Nests were not visited when snow covered the vegetation around the nest, when tracks of an observer can artificially increase predation risk. When nests were found after laying or hatching, egg initiation was determined by back-dating. Nestling age was estimated from morphological measurements and we assumed an incubation time of 15 days (Bollmann 1996). Incubation starts with the last egg, and the laying interval is 24 hr.

Prey biomass. Territory-specific prey biomass was calculated from vegetation-specific prey biomass, which was measured twice per season (June 17–24 and July 14–27) by sweep netting, using a 50 × 50 m grid on a topographical map (1:5000) of the study area. This technique guarantees adequate sampling of the five most important prey taxa (77% of the nestling food in neck-collar samples, Brodmann 1995). Further details about prey sampling and the calculation of territory-specific, size-independent prey biomass are given by Brodmann (1995), Bollmann et al. (1997), Brodmann et al. (1997), and Bollmann and Reyser (1999).

Measures of reproductive success. All nests receiving at least one egg were considered as breeding attempts. For each female we determined the number of breeding attempts, the laying dates, hatching dates, fledging dates, clutch size, and the number of young hatched and fledged. Fledgling numbers refer to the number of nestlings that reached banding age (7–10 days) and were not depredated or found dead in or near the nest at fledging age (10–18 days, mode = 14). A successful nest was one that produced at least one fledgling. Clutch size, number of young fledged per brood and number of young fledged per season and female were used as measures of reproductive success.

Nest predation. We classified the causes of nest predation either through direct observation or indirectly through predator-specific signs at or around the nest site. Pietz & Granfors (2000) have shown that up to 15% of such predator classification by signs can be wrong. In our study area, however, the combination of signs left on nests, nestlings, and incubating females differed among predators. This, and our knowledge of the potential predators' activity patterns in space and time (e.g., adders confined to the southwest slopes, diurnal adders vs. nocturnal stoats) made the probability of misinterpreting the causes of nest failure very small. According to our classification of 123 nest losses, 37 of them partial (≥ 1 egg or nestling) and 86 total, the main predators were adder (*Vipera berus*; 40%), stoat (*Mustela erminea*; 30%), red fox (*Vulpes vulpes*; 10%), carrion crow (*Corone corone*; 7%), and mouse (unknown spp.; 5%). Losses were also caused by domestic dog (*Canis aureus*; 2%), badger (*Meles meles*; 1%), and from nest parasitism by Cuckoos (*Cuculus canorus*; 1%). The amount of undefined nest losses amounted to 5%.

STATISTICAL ANALYSES

First, replacement, and second clutches were used in the analyses of breeding phenology and reproductive performance ($n = 387$). Sample sizes differ slightly between analyses because after nest failure or nest desertion, some laying dates could not be ascertained exactly. Where the influence of female age on reproductive performance was tested, only one breeding season per female was used. The choice was based on a random number table.

We used analyses of variance and analyses of covariance for relating clutch size, the number of

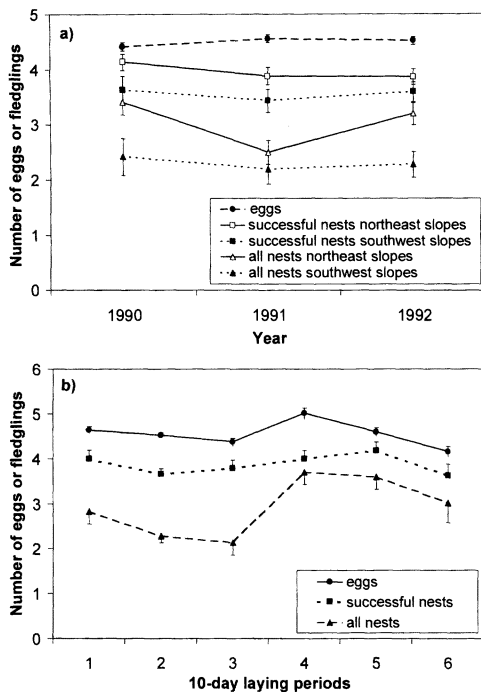


FIGURE 1. Reproductive performance of Water Pipits in eastern Switzerland, measured as mean (\pm SE) number of eggs or number of fledglings per nest, in relation to (a) year and slope and (b) 10-day laying periods within the breeding season.

young fledged per brood, and the number of young fledged per season to time (year, laying date), space (slope) and their interactions. We also explored through a stepwise ANCOVA how predation, precipitation, prey density, and female age affected reproductive success. Although data on

prey density and female age were available for 1991 and 1992 only, analyses using this reduced data set did not differ from the one presented below for all three years. Prey index and female age were among the first variables excluded during the stepwise procedure. We used logistic regression to test the effect of year, slope, laying date, clutch size, and reproductive success in the first brood on the probability of renesting.

Nonparametric statistics were used where requirements for parametric tests were not fulfilled. Estimates of errors are standard errors (SE) unless otherwise stated. Pairwise comparisons are two-tailed. Statistical significance was accepted at $P < 0.05$. Statistics were calculated using Systat 7.0 for Windows (SPSS 1997).

RESULTS

Over the three years of the study, we monitored 387 broods; 237 (61%) were found before or during incubation and the others during the nestling period. The combined number of eggs and nestlings in late-detected broods did not differ from clutch size in early-found nests for any one year (ANOVA: $F_{1,385} = 0.6$, $P > 0.4$). Therefore, we pooled data from nests found before and after hatching for all three years for further analyses.

REPRODUCTIVE SUCCESS IN SPACE AND TIME

Average clutch size was 4.51 ± 0.04 , with no significant differences between slopes and years (Fig. 1a, Table 1). Yet, the mean number of fledglings was significantly lower at the southwest than at the northeast slope, for all nests

TABLE 1. Results from an ANOVA (excluding the covariate laying date) and three ANCOVAs relating laying date, clutch size, fledglings per nest and fledglings per successful nest to year, slope, their interaction, and laying date of the first egg in the first clutch. Because of the polynomial relationship between reproductive success and date of clutch initiation (see Fig. 1b), laying date was also entered as a quadratic term (laying date)² and a cubic term (laying date)³.

Independent variable	Number of fledglings								
	Laying date (of first clutch)			Clutch size (all nests)		(all nests)		(successful nests)	
	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Slope	1	26.1	<0.001	0.2	>0.6	9.6	0.002	5.9	<0.02
Year	2	48.2	<0.001	1.1	>0.3	1.3	>0.2	0.4	>0.6
Slope × year	2	0.6	>0.5	0.4	>0.7	0.9	>0.4	0.1	>0.8
(Laying date)	1			17.2	<0.001	20.6	<0.001	7.6	<0.01
(Laying date) ²	1			18.2	<0.001	21.7	<0.001	8.1	<0.01
(Laying date) ³	1			19.3	<0.001	22.7	<0.001	8.5	<0.01
Error df		204			350		350		244
<i>R</i> ²		0.37		0.09		0.15		0.09	

(2.31 ± 0.16 vs. 3.00 ± 0.13) and successful nests only (3.57 ± 0.13 vs. 3.97 ± 0.08). Fledging success appeared to be lower in 1991 than in the other two years, but the year effect was not significant (Fig. 1a, Table 1). Including nests for which the date of clutch initiation was not exactly known (i.e., without laying date as a covariate), also indicated that slope affected fledgling numbers for all nests (ANOVA; $F_{1,381} = 16.3$, $P < 0.001$) and for successful nests only ($F_{1,247} = 6.4$, $P < 0.02$). The year effect on fledgling numbers in the all-nests sample became more obvious ($F_{2,381} = 3.9$, $P < 0.07$), with pairwise comparisons suggesting that fledging success in 1991 was lower than in 1990 (Scheffé test, $P < 0.08$).

In terms of seasonal breeding phenology, the initiation of the first clutch varied with both slopes and years (Table 1). On average, first eggs appeared about 4 days earlier at the southwest than at the northeast slope (29 May vs. 2 June). Pooled over both slopes, laying varied from 5 June in the cold year 1991 through 31 May in 1992 to 27 May in the warm year 1990, with significant differences between all years (Scheffé test, $P < 0.001$ for all 3 pairwise comparisons). In none of the four analyses was there a significant slope \times year interaction (Table 1). This indicates that the annual effects on timing and success of reproduction did not differ between slopes and the slope effects were consistent among years.

Since termination of laying mirrored the annual and spatial differences in clutch initiation, length of the total laying period varied very little. The number of days from the first egg until the last egg in the population was laid averaged 47.8 ± 2.6 (SD) days (range 44–51) with no significant differences between the three years ($F_{2,2} = 0.01$, $P > 0.9$) or the two slopes (ANOVA, $F_{1,2} = 0.01$, $P > 0.9$). Within this total laying period, however, slopes differed in the frequency distribution of clutch initiation date and in the relative numbers of first and second clutches. At the northeast slope there was a higher proportion of second clutches $\chi^2_2 = 8.5$, $P < 0.02$, which explains the peak in the fifth 10-day period (Fig. 2).

Clutch size and fledgling number also varied during the season (Table 1): they were higher for broods initiated later (10-day periods 4–6) than in those started earlier (periods 1–3) (Fig. 1b). These seasonal differences were small for

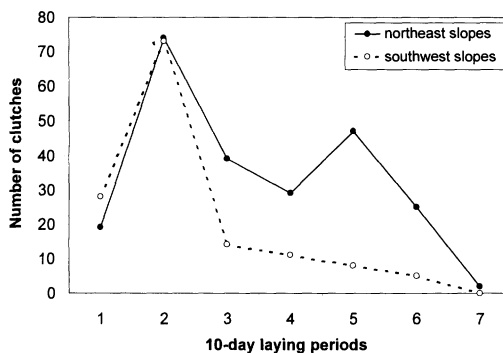


FIGURE 2. Number of Water Pipit clutches initiated on the northeast and the southwest slopes of the Dischma Valley, Switzerland, in relation to time of the season, expressed by 10-day laying periods. Start date of period one = 15 May.

clutch size and number of fledglings from successful nests but marked for number of fledglings from all nests. This suggests that differences in reproductive success between early and late breeding periods are mainly due to varying rates of nest loss.

ECOLOGICAL AND DEMOGRAPHIC DIFFERENCES BETWEEN SLOPES, YEARS, AND SEASONAL PERIODS

Out of the 387 nests that were monitored between 1990 and 1992, 254 (66%) fledged at least one young. Predation and harsh weather together accounted for 83% of nest losses. Other causes of nest failure included unfertilized eggs, starvation, and abandonment of nests (usually by secondary females of polygynous males). Below, we investigate four factors that may have contributed to reproductive differences in space and time. For the first two (nest predation and precipitation) we have data from all three study years; data on the second two (food availability and female age) are available for 1991 and 1992 only.

Nest predation. Predation on eggs and nestlings was by far the dominant cause (65%) of total nest failure. Predation rates differed between the two sides of the valley. A much higher proportion of broods was depredated on the southwest than on the northeast slope (53% vs. 11%; $\chi^2_1 = 57.6$, $P < 0.001$). Predation rate did not vary strongly among years ($\chi^2_2 = 1.9$, $P > 0.3$), but was higher in laying periods 1–3 than in 4–6 (36% vs. 14%; $\chi^2_1 = 13.2$, $P < 0.001$). This, however, is a spurious seasonal effect, con-

TABLE 2. Results from two stepwise ANCOVAs relating number of fledglings per nest and per season to the independent variables and interactions listed in the left column. *F* and *P*-values are shown only for significant variables and interactions which remained in the model after stepwise backward elimination^a.

	df	Number of fledglings			
		Per nest		Per season	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Predation	1	245.1	<0.001	56.7	<0.001
Precipitation	1	99.8	<0.001	24.3	<0.001
Slope	1			20.3	<0.001
(Laying date)	1			13.0	0.003
Year × (laying date)	2	5.5	0.005		
Year × (laying date) ²	2	6.0	0.004		
Slope × year × (laying date)	2	11.1	<0.001	9.3	<0.001
Slope × year × (laying date) ²	2	10.9	<0.001		
Error df		264		230	
<i>R</i> ²		0.62		0.47	

^a The complete model also included year, slope × year, (laying date)², (laying date)³, slope × (laying date), slope × (laying date)², slope × (laying date)³, year × (laying date)³ and slope × year. The quadratic term (laying date)² and the cubic term (laying date)³ were entered into the analysis because of the polynomial relationship between reproductive success and clutch initiation.

founded by differences between the two slopes. The southwest slope, where predation was frequent, had few active nests in periods 4–6, whereas the northeast slope, with its lower predation rate, had more active nests in periods 4–6 (Fig. 2). When the two slopes are tested separately, the difference in the rate of nest predation between early and late breeding periods disappears (northeast: $P > 0.1$; southwest: $P > 0.6$).

Precipitation. At 18% of nest failures, precipitation was the second most frequent cause of total nest loss. In contrast to nest predation, the effects of rain and late snowfalls on reproductive success varied with time, both among years and within seasons. The proportion of nests lost to snowfall and rain was much higher in 1991 (20%) than in 1990 and 1992 (2.1% and 1%, respectively, $\chi^2_2 = 35.3$, $P < 0.001$), and it was higher during laying periods 1–3 than in periods 4–6 ($\chi^2_1 = 4.3$, $P < 0.04$).

Food availability. Territory-specific food availability during laying periods 1–3 was 49% higher on the southwest than the northeast slope (ANOVA; $F_{1,192} = 45.0$, $P < 0.001$) but did not differ between 1991 and 1992 ($F_{1,192} = 0.02$, $P > 0.8$). Food availability increased by 81% from the first to the second half of the breeding season ($F_{1,258} = 46.7$, $P < 0.001$), but the seasonal increase was higher in 1991 (130%) than in 1992 (35%; $F_{1,258} = 14.9$, $P < 0.001$ for the year × breeding period interaction).

Age of females. For 204 of the 387 nests we knew the age class of the females initiating clutches (second-year vs. after-second-year). The age distribution differed between the two sides of the valley and between early and late timing of first clutches. The proportion of older females was higher at the northeast than at the southwest slope (36% vs. 24%; $\chi^2_1 = 3.9$, $P < 0.05$) and higher during laying periods 1–2 than in periods 3–4 (39% vs. 16%; $\chi^2_1 = 7.4$, $P < 0.01$). On average, after-second-year (i.e., experienced) females initiated their first clutches 3 days earlier than second-year females.

FACTORS CAUSING TEMPORAL AND SPATIAL DIFFERENCES IN REPRODUCTIVE SUCCESS

The number of fledglings per nest (Table 2) was negatively affected by predation and precipitation (both $P < 0.001$) and also depended on the interaction between year, slope, and laying date of the first clutch. The analysis for the total number of young fledged per season (Table 2) confirmed the strong effects of predation and precipitation (both $P < 0.001$) and the interaction between year, slope, and laying date ($P < 0.001$). However, the precise seasonal pattern differed between the two reproductive measures.

Success per nest depended not only on laying date, but also on its quadratic term (Table 2), because fledgling numbers peaked at intermediate laying dates (Fig. 3). For the northeast slope, this was the case in all three years. The

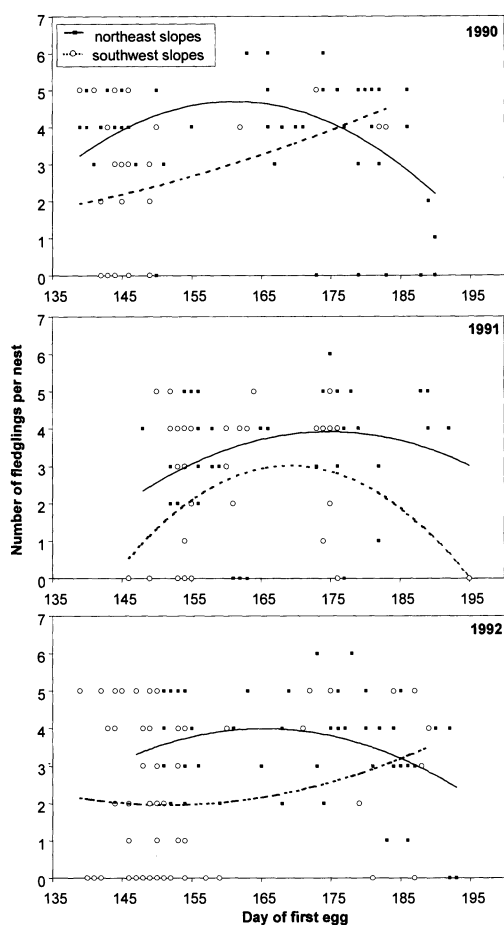


FIGURE 3. Number of Water Pipit fledglings reared per nest in relation to the day of clutch initiation during 1990–1992 in eastern Switzerland. Squares and solid lines refer to the northeast slope, circles and broken lines to the southwest slope. For statistical information see Table 2.

equations were $y = -0.003x^2 + 0.968x - 73.2$; $y = -0.002x^2 + 0.772x - 63.5$; and $y = -0.002x^2 + 0.679x - 52.1$ for 1990, 1991, and 1992, respectively, where y is the number of fledglings and x the day of the first egg. For the southwest slope this relationship was present only in 1991 (Fig. 3b), when the relationship followed the equation $y = -0.005x^2 - 1.548x - 128$. In 1990 and 1992 (Fig. 3) success per nest increased from early to late broods (1990: $y = 0.001x^2 - 0.337x + 27.5$; 1992: $y = 0.001x^2 - 0.337x + 27.5$). As a result, there was a significant slope \times year \times laying date interaction.

For annual success (Table 2), the interaction containing the quadratic term was excluded from

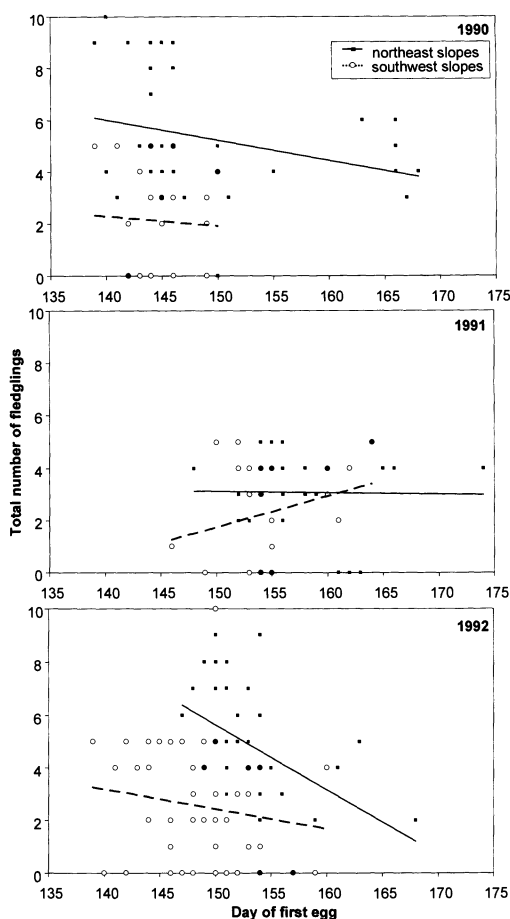


FIGURE 4. Total number of Water Pipit fledglings reared per year in relation to the day of first clutch initiation during 1990–1992 in eastern Switzerland. Squares and solid lines refer to the northeast slope, circles and broken lines to the southwest slope. For statistical information see Table 2.

the model, and only the linear seasonal component remained: the earlier the first clutch was initiated, the higher the annual reproductive success ($P < 0.005$). Again, a significant slope \times year \times laying date interaction showed that the time effect varied between slopes and years (Fig. 4). On both sides of the valley, the strength of the relationship was strongest in 1992 and weakest in 1991. In any one year the negative effect of the progressing season on fledgling number tended to be more pronounced on northeast than southwest slopes. The regression equations for the northeast slope were $y = -0.079x + 17.1$; $y = -0.006x + 3.9$; and $y = -0.247x + 42.7$ for 1990, 1991, and 1992, respectively. The corre-

TABLE 3. Results from a stepwise logistic regression relating the probability of reneesting to the independent variables listed in the left column. Statistical values are shown only for significant variables which remained in the model after stepwise backward elimination. The original model also included the variables year and clutch size. Inclusion of food availability and female age as independent variables did not change the final model. The coefficients indicate how much the logit changes for a unit increase in the respective independent variable.

	Coefficient	SE	<i>t</i> -ratio	<i>P</i>
Laying date	-0.12	0.03	-3.54	<0.001
Number of fledglings from first brood	0.72	0.14	3.98	0.002
Slope	0.49	0.21	2.30	0.02
Log likelihood	$\chi^2_3 = 22.7, P < 0.001$			

sponding equations for the southwest slope were $y = -0.038x + 7.5$; $y = 0.120x - 16.3$; and $y = -0.076x + 13.8$.

The overall negative seasonal effect was mainly due to the declining probability of reneesting with later laying. Among 183 females that we followed closely after loss or successful completion of their first clutch, 46 (25%) reneested. Reneesting did not depend on year or clutch size of the first brood, but was significantly related to the laying date of the first clutch and to the number of young that had fledged from the first brood (0 to 6 fledglings, Table 3). Females that did reneest had laid their first egg on average three days earlier than those that did not reneest. The proportion of females reneesting was slightly higher at the northeast than at the southwest slope (27% vs. 24%) and was markedly higher among females that lost their first brood than among those that successfully fledged young (41% vs. 21%). In a second analysis, prey density and female age data from

1991 and 1992 were included, but had no significant influence on probability of reneesting.

After adding brood history as an additional independent variable (1 = only one brood, 2 = first (failed) + replacement brood, 3 = first and second broods), laying date was no longer significant, but brood history was (t -ratio = -6.95, $P < 0.001$). The average number (\pm SE) of young fledged per season increased from females with only first broods through females with replacement clutches to females with two breeding attempts (Fig. 5). Hence, the main advantage of early breeding lies in producing a second brood after the first has fledged, or a replacement clutch if the first fails.

DISCUSSION

Nest predation and harsh weather were the main proximate causes of differences in female reproductive success in the multi-brooded Water Pipit. Within a given period and locality, these factors are fairly unpredictable; but since they are related to season and area, females can to some extent control their effects by choosing when and where to breed.

TIME OF BREEDING

Lack (1968) stated that females attempting more than one brood per season should nest as early as possible, and the advantage of such early breeding was later documented by several empirical studies (Stutchbury and Robertson 1988, Verboven and Verhulst 1996, Siikamaki 1998). However, birds of alpine environments find themselves in a narrow breeding window restricted by a high probability of snowstorms in spring and autumn. These storms can cause high adult mortality (Nilsson 1994) and partial or total nest loss (Morton et al. 1972, Wartmann 1985, King and Mewaldt 1987). Moreover, settling too early can complicate assessment of pre-

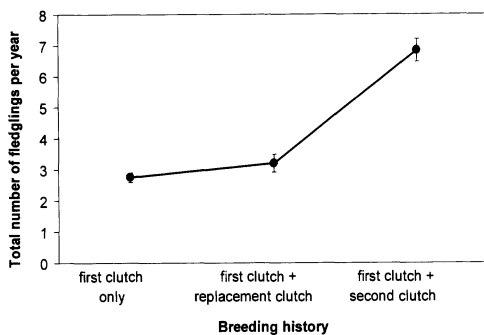


FIGURE 5. Mean (\pm SE) number of Water Pipit fledglings reared per female per year in relation to breeding pattern: first clutch only = females bred only once; first clutch + replacement clutch = females initiated a new clutch after failure of the first nest; first clutch + second clutch = females started a second brood after a successful first breeding attempt.

dation risk because cues revealing risk are hidden below snow (Bollmann et al. 1997). Hence, breeders face a trade-off between losing first broods due to an early start and losing the chance of a second brood due to a late start. The optimal solution for this trade-off depends on local temporal and spatial patterns of ecological conditions.

In our study area, the predation rate did not differ significantly between early and late broods within a slope. This result contrasts with some other studies on open-nesting species that found a decrease during the breeding season (Newton 1972, Gottfried and Thompson 1978, Temrin and Jacobsson 1988). The probability of snowstorms, however, decreased as the season progressed, reaching its lowest level in July and August (Bollmann 1996). Yet, most females did not delay breeding until this climatically benign period, but started laying in late May or early June. In spite of the high chance of losing their first brood and the lower number of fledglings per nest (Fig. 3), birds starting to breed early fledged more young per season than late breeders (Fig. 4). This is because early breeders could often initiate a replacement clutch after nest failure or, less often, a second brood after a successful first brood (Fig. 5).

BREEDING AREA

Next to time of breeding, the choice of the breeding area had the largest effect on reproductive success because of differences in predation and microclimate. Females breeding on the southwest slope suffered a high rate of nest predation by adders. This key predator was absent from the northeast slope. In contrast, losses through mammalian and avian nest predators did not differ in space and time (Rauter et al. 2002). Within the distribution area of the adder, we could not find an environmental correlate for the occurrence of nest predation, and birds settled independently of later predation; i.e., territories with low predation rates were not filled earlier than those with high predation rates (Bollmann et al. 1997), probably because local adder distribution could not be assessed at the time of settlement. Predation is also an important factor influencing territory quality and reproductive success in other open-nesting songbirds (Weatherhead and Robertson 1977, Temrin and Jacobsson 1988, Askenmo and Neergaard 1990).

Females breeding at the northeast slope also

enjoyed a more favorable nest climate than those at the southwest slope. Nest temperatures at the northeast slope were characterized by lower extreme values and less diurnal variation. Standard operative temperatures measured in the nests revealed average daily maxima of 18°C for the northeast and 25°C for the southwest slope during the nestling period of first broods and 26°C and 35°C, respectively, during the nestling period of second broods (Rauter and Reyer 2000). In ground-nesting birds, heat stress is a cause of nestling mortality (Salzmann 1982, Murphy 1983), and Water Pipit nests on the northeast slope, with its more moderate microclimate, fledged more young than those on the southwest slope (Fig. 1; Rauter et al. 2002). Because the temperature conditions on the southwest slope became more extreme during the summer, they probably contributed to the smaller proportion of second broods on this slope. This increase in adverse climatic conditions must have been particularly pronounced during the three years of our study. Compared to the ten preceding years, summers (July–August) but not springs (May–June) had 1.45°C-higher average air temperature, 20 mm less rain, 74 mm less new snow and 0.8 fewer days with maximum temperature below 0°C (Bollmann 1996).

Territory-specific food availability, which is a good reflection of nestling food (Brodmann 1995), did not explain variation in reproductive success per nest or per season, in contrast to several other studies (Martin 1987, Tinbergen and van Balen 1989). There are probably two reasons for this result. First, Water Pipits do not feed exclusively within their territories. About 50% of all food is collected in common feeding grounds. This behavior decreases the differences in prey biomass that exist between territories and slopes (Frey-Roos et al. 1995, Bollmann et al. 1997). Second, food abundance was apparently not a limiting resource in our study area. Only 3% of all nestlings from 6.8% of the nests were judged to have died through starvation (Bollmann 1996). Hence, brood reduction, which is seen as an adaptive response to marginal breeding conditions in altricial birds (Lack 1947, Magrath 1989, Mock and Forbes 1995), did not occur in our population.

In summary, although the southwest slope was better than the northeast slope in terms of food availability and allowed breeding to start 4 days earlier on average, these advantages did not

compensate for the lower nest predation frequency and the better climatic conditions at the northeast slope later in the breeding season. Hence, early breeding in general, and especially in an area with a predictable and low probability of nest predation, was the best strategy to improve reproductive success in a locally unpredictable alpine environment. This results in the prediction that females returning to the same area can profit from their previous year's experience through earlier settlement and choice of the better northeast slope. Interestingly, overall density and proportion of older females was indeed higher on the northeast than on the southwest slope. However, the sample size of banded females changing slopes from one year to the next is much too small ($n = 5$) to test whether the change is in the expected direction. Changes may be rare because experience with a specific territory may outweigh differences in habitat quality, or options for settling elsewhere may be restricted by competition with conspecifics or because benefits from changing slopes may vary from year to year. In years when snowstorms are frequent and severe and food availability is restricted, breeding on the southwest slope could be favored, because the effects of snow and food availability on reproductive success may outweigh those of predation risk.

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