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Selection through predation, snowfall and microclimate on nest-site preferences in the Water Pipit *Anthus spinoletta*

CLAUDIA M. RAUTER,[1,2,3] HEINZ-ULRICH REYER[1]* & KURT BOLLMANN[1,4]
[1] *Institute of Zoology, and*
[2] *Zoological Museum, University of Zurich, Winterthurerstr. 190, CH-8057 Zurich, Switzerland*

Nest-site characteristics can have a strong impact on reproductive success in birds. Nest sites should simultaneously protect from predators, offer shelter and provide a favourable microclimate. We studied the relationship between three agents of natural selection (predators [i.e. Adders and birds/mammals], snowfall and microclimate), nest-site characteristics and reproductive success to determine whether these influenced preference for specific nest-site characteristics in the Water Pipit *Anthus spinoletta*. Pooled over all nests, the relative importance as agents of natural selection decreased from mammalian/avian predation (15% of all nests) through Adder predation (12%) to snowfall (7%), but there were clear differences in space and time. Predation by Adders selected for nest sites surrounded by few medium-sized shrubs. Selection by mammalian and avian predators favoured no specific nest-site characteristics. Protection from snowfall was best in nests surrounded by relatively few medium-sized shrubs. Microclimate had a strong influence on nestling survival and duration of nestling period. In nests on ENE-facing slopes, where maximum temperatures were reached in the morning, nestling survival was higher than on WSW-facing slopes, where temperature maxima occurred in the afternoon. Our results indicate that weak, but significant, directional selection is acting on preference for certain nest-site characteristics through effects on survival and development of nestlings. As predation and snowfall are unpredictable, the evolution of an optimal nest placement strategy is unlikely on a small scale. On a larger scale, however, choice of one breeding area over another may be favoured because of predictable differences between locations in terms of survival and nestling development.

The characteristics of a nest site can have a strong impact on reproductive success in birds (Collias & Collias 1984, Martin 1992). The characteristics of a nest site may reduce the risk of predation, but the specific nest-site characteristics that improve safety can vary with the searching behaviour of predators (e.g. Martin 1988, Clark & Nudds 1991, Martin 1992, Hatchwell *et al.* 1999, Hooge *et al.* 1999). A nest site providing protection from inclement weather like heat waves, cold spells, rain storms or snow may reduce losses of individual eggs or nestlings and the likelihood of complete nest failure (Lawton & Lawton 1980, Salzman 1982, Collias & Collias 1984, Penloup *et al.* 1997). Nest sites which improve the microclimate may provide thermal benefits to the eggs and nestlings (Webb & King 1983), reduce the energetic costs of nesting birds (Haftorn & Reinertsen 1985, Walsberg 1985, Chappell *et al.* 1990) and, hence, can result directly or indirectly in higher reproductive success (e.g. Austin 1976, Wachob 1996).

An optimal nest site should provide protection from predators, shelter from inclement weather, and a favourable microclimate for eggs, young and incubating or brooding parents. However, the need for security, shelter and favourable microclimate can cause opposing selection pressures on nest placement (Lawton & Lawton 1980, Murphy 1983, Marzluff 1988, Halupka 1998). Knowing the relative importance of predation, weather, and microclimate

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*Corresponding author.
E-mail: ulireyer@zool.unizh.ch

Present addresses: [3]Department of Entomology, University of Kentucky, Lexington, KY 40546–0091, USA. [4]Division of Biodiversity, Swiss Federal Institute WSL, Zuercherstrasse 111, CH-8903 Birmensdorf, Switzerland.

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in determining nest placement and the specific features of nest sites they favour is therefore basic to understanding how natural selection shapes the choice of nest sites in birds.

Ground-nesting birds breeding at high elevations provide excellent opportunities to investigate these relationships. These birds face not only high predation pressure but also cold spells and snow storms which are not unlikely during the breeding season and can result in partial or complete nest failure (e.g. Verbeek 1970, Morton *et al.* 1972, King & Mewaldt 1987, Hendricks & Norment 1992, Bollmann *et al.* 1997). Furthermore, air temperature close to the ground regularly fluctuates between high and low extremes. During daytime, it can reach levels higher than the upper lethal temperature of eggs, while at night it may fall below 5 °C or even below 0 °C (Swan 1952, Hadley 1969, Franz 1979, Webb & King 1983), causing increased thermoregulatory costs for the adult bird (Haftorn & Reinertsen 1985). To investigate how predation, inclement weather and microclimate influence the placement of nests, we investigated their impact as agents of natural selection on nest-site characteristics and its consequences for fitness correlates in Water Pipits *Anthus spinoletta*.

Water Pipits, small insectivorous passerines, are common ground-nesting birds in the Alps above the timberline (Glutz von Blotzheim & Bauer 1985). The females place their cup-shaped, grass nests into a hollow underneath a shrub, sod or rock. The hollow and the cover provided by the material surrounding it (roots of a shrub, overhanging grass or soil) form a shelter for the nest (Böhm & Landmann 1995) and determine the microclimate in the nest cavity (Rauter & Reyer 2000). Snowfall during the Water Pipits' breeding period is common, and one of the main causes of nest failure (Glutz von Blotzheim & Bauer 1985, Bollmann *et al.* 1997). Predation can be another important cause of partial or complete nest failure. At our study site, an Alpine valley, the main predators are Adders *Vipera berus*, Red Foxes *Vulpes vulpes*, Stoats *Mustela erminea*, and Carrion Crows *Corvus corone* (Bollmann *et al.* 1997).

To investigate how predation by different types of predators (i.e. Adders and birds/mammals), late snowfall and microclimate might influence nest-site selection in Water Pipits, we determine in this paper the relationship between these three selection factors, 12 nest-site characteristics and reproductive success. We also consider the effects of food availability and feeding rates which, together with microclimate, affect the energy budget of the nestlings.

METHODS

Study area and birds

The study was carried out between 1990 and 1992 in the central Alps of eastern Switzerland near Davos in the valley of 'Dischma' which runs from SSE to NNW. The study area covered a 200-ha cross-section through the valley and was above the timberline at an elevation of 1800–2400 m. The valley floor is characterized by meadows. On the WSW-facing slope of the study area the vegetation is dominated by Heather *Calluna vulgaris* and Juniper *Juniperus communis*. The ENE-facing slope is covered on its lower and middle parts mainly by Rhododendron shrubs *Rhododendron ferrugineum* and on its upper parts by Trailing Azaleas *Loiseleuria* sp. and lichen.

As a short-distance migrant, the Water Pipit returns to our study site in April and starts breeding according to the pattern of snow melt (Bollmann *et al.* 1997). Thus, females do not build nests until late May or early June. Females lay 4–5 eggs on average and incubate them alone. Some males support their incubating females by providing them with food. After about 15 days the young hatch. Both parents feed the nestlings, but only the female broods the young. The average nestling period amounts to 15 days (Bollmann 1996, Rauter 1996).

Agents of natural selection and nest-site characteristics

Microclimate

When the nestlings were 1–7 days old, a thermocouple (NiCr–Ni, Thiele, Ingenieur-Büro für Messtechnik GmbH, München, Germany) was placed 2 cm underneath the nest cover above the centre of the nest. The thermocouple had no contact with nestlings or adults. The temperature measurements were stored by a Rustrak recorder (Thiele) which was placed in a wooden box 2–5 m away from the nest cavity. One-minute recordings were used to calculate hourly means of temperatures. From the hourly means we identified minima and maxima for 24-h periods lasting from 05 : 00 h CET until 05 : 00 h CET the next day. The results were then used to calculate the average of the minimum and maximum temperatures for each of 33 nest cavities over a period of 3–12 days (mean = 5 days). We used the average of the minimum and maximum temperatures measured for each nest rather than the most extreme values measured in each nest to reduce the effect of rare, but extreme, weather conditions on the estimate of the thermal conditions. We also determined for each nest the average of mean nest temperature at night (20 : 00–05 : 00 h, CET) and the average of the mean nest temperature by day (05 : 00–20 : 00 h, CET).

To control for weather effects we regressed mean temperature at night and the average of the minimum temperature, respectively, on mean air temperature at night and used the residuals in the analyses. Similarly, we regressed mean daytime temperature and the average of the maximum temperature, respectively, on mean daytime air temperature and used the residuals in the analyses. Air temperature was measured by a thermistor (Type AT1, Delta-T Devices Ltd, Cambridge, UK) located 2 m above ground in the centre of the study area. Every 10 min air temperature was recorded and hourly means were stored by a logger (Type DL2, Delta-T Devices Ltd). The hourly means were used to calculate mean air temperature during the day (05 : 00–20 : 00 h, CET) and night (20 : 00–05 : 00 h, CET) for each nest. None of the temperature measurements in the nest cavity was correlated with brood size (all $P > 0.251$). Hence, brood size was not included in the analyses. We performed all analyses with minimum and maximum temperatures or mean temperatures at night and day. The results were the same for both analyses; therefore, we report only the results of the analyses using minimum and maximum temperatures. Sample sizes for nest temperature measurements in 1990, 1991 and 1992 were one, nine and 14 nests, respectively, for the ENE slope and one, two and four nests for the WSW slope. As a third measure to describe the thermal microclimate we used a factor indicating whether the temperature maximum occurred before midday or in the afternoon. At the ENE slope the temperature maximum occurred about 2–3 h after the first sun rays reached the slope. On the WSW slope temperature maxima were reached in the late afternoon (Rauter & Reyer 2000).

Security from predation

A nest was scored depredated by an Adder when the snake was observed feeding on nestlings, when nestlings covered with slime were found dead in or around the nest or when some or all nestlings had disappeared without any visible damage to the nest. After a predation event, the surroundings of the nests were searched for parents feeding offspring nearby, to determine the number of nestlings that survived the attack by leaving the nest prematurely. Because Adders occur only on the WSW slope of the valley (pers. observation) only nests from this slope were included in the analyses of the strength of selection exerted by Adder predation on nest-site characteristics. This analysis is based on a total of 103 nests of which 40 (39%) had been depredated by Adders. In no case was a parent bird also taken.

A nest was considered depredated by a mammalian or avian predator if all nestlings or part of them had disappeared and the nest was damaged or destroyed, or if parts of the female or its feathers were found near the nest. The nature of the predator was deduced from knowledge of the potential predators' activity patterns in space and time and a combination of marks left on nests, chicks and/or breeding females (Bollmann & Reyer 2001). According to this classification, mammalian predators included Stoats (29 nests), Red Foxes (13 nests) and dogs (two nests), while avian predators were only Carrion Crows (seven nests). Hence, the analysis of selection exerted by mammalian and avian predators is based on a sample of 51 depredated nests which are compared to 204 unpredated ones. In five of the 51 predation cases the female parent was also killed.

For the selection gradient analysis (see below) predation by Adders and predation by birds and mammals were given the same weight, because the effects were similar: both predator categories usually only took nestlings, caused more total than partial loss and, in the case of partial loss, took the same toll of 1–4 nestlings.

Shelter from snow

In mid-June 1991 a late snowfall destroyed 22 of 80 active nests (i.e. 28%). Such nest loss due to precipitation is a regular event in this alpine habitat. Next to predation it represents the second most frequent cause of reproductive failure (Bollmann & Reyer 2001). In the analyses of the strength of selection of late snowfall, only nests containing eggs or nestlings at onset of this snowfall were included.

Nest-site characteristics

With respect to safety from predation and shelter from snow each nest site was characterized by the following 12 environmental variables for which data were collected at the end of the breeding season in each year.

1 *Bottom of the nest cavity*, scored as 'earth', 'rock' and 'vegetation' (i.e. roots), depending on which material dominated.

2 *Cover of the nest cavity*, scored in the same way as the bottom according to the dominating material.
3 *Relative orientation of the entrance to the nest cavity*, expressed as the difference between the orientation of the slope of the valley and the orientation of the fall line that bisected the entrance of the nest cavity. Positive values indicate that the entrance of the nest cavity faced the entrance of the valley, and negative ones show that it was orientated away from the entrance of the valley.

The topography within a 0.5-m radius circle of each nest was described by nine variables, with 4–10 providing estimates of the area covered by vegetation and other material. To estimate the percentage coverage by a certain vegetation type or material, we used a cross. Each of the four arms of the cross was 50 cm long, and 10-cm intervals were marked on the arms. We put the centre of the cross over the nest and estimated how many 10 × 10-cm squares were covered by a certain vegetation type or material. Because of the highly skewed distributions of all these variables 4–10, their percentage values were transformed into dichotomous variables by assigning the value 0 to all values smaller than the median and the value 1 to all values equal or greater than the median.
4 *tall dwarf shrubs* (*Juniperus communis* and *Rhododendron ferrugineum*),
5 *medium-sized dwarf shrubs* (*Calluna vulgaris*, *Vaccinium myrtillus* and *Vaccinium uliginosum*),
6 *small dwarf shrubs* (*Vaccinium vitis-idaea*, *Arctostaphylos*, *Empetrum*), including herbs,
7 *grass*,
8 *ground covering vegetation* (*Loiseleuria*, moss, and lichen),
9 *bare ground*,
10 *rock*.

Within a 0.5-m radius of the nests, we also noted the *average height of rocks* (m) which could serve as potential lookouts for the Water Pipits or predators.

Further, we measured the *inclination of the slope* at the nest site, because Water Pipits prefer steep slopes over flat areas (Böhm & Landmann 1995).

In 1990 we collected data on nest-site characteristics from 42 nests on the ENE slope and 35 nests on the WSW slope. The corresponding sample sizes were 72 and 50 nests in 1991 and 69 and 57 in 1992. Owing to differences in the completeness of the data set, sample sizes for nest-site characteristics varied slightly: 409 nests for bottom and 408 nests for cover of nest cavities, 411 nests for relative nest orientation, 405 nests with data on ground cover, and 413 nests with inclination of slope.

Food availability and feeding rates

As a measure for food availability we used arthropod biomass, assessed by sweep netting. Samples were taken according to a 50 × 50-m grid system that was drawn onto the map of the study area. All squares were sampled once between 17 and 24 June, the period when most of the first broods are in the nestling stage, and once between 14 and 21 July, the period when most replacement and second broods had nestlings. For recording feeding rates, nests were continuously observed over a period of 2–5 h when the nestlings were 6–8 days old. Further details for these methods are given by Brodmann *et al.* (1997), Brodmann & Reyer (1999) and Rauter *et al.* (2000).

Correlates of fitness

All nests were found either during nest construction or incubation. Thus, for all nests clutch size, number of hatchlings and hatching date were known. We visited the nests every 2–4 days during the incubation and nestling periods. When hatching or fledging was expected, we checked the nests daily.

Survival of a complete brood from hatching to fledging

For the analyses estimating the effects of predation by Adders, mammals and birds, and loss through late snowfall we assigned a nest a survival value of 0 when at least one nestling was lost through any of these causes; otherwise nests were assigned a survival value of 1. We treated partial and complete nest losses equally because partial nest losses resulted, on average, in a loss of about 50% of the brood. The average percentage of broods lost to snow was 50% (one nest with partial losses), to predation by mammals or birds 54% (seven nests with partial losses) and to Adder predation 50% (17 nests with partial losses).

Nestling development

The fitness correlates measured in the analysis testing for the effects of microclimate were number of fledglings, duration of the nestling period (time between the day most eggs hatched and the day most chicks fledged), and mean body weight and tarsus length for each brood. We considered the duration of the nestling period as a fitness correlate, because shorter nestling periods are associated with higher predation rates resulting in a reduction in the vulnerable period (Martin 1995, Halupka 1998).

The body weights and tarsus lengths of nestlings were measured when the nestlings were 8–11 days old, about a week before they left the nest. To control for age effects, both body weight and tarsus length were standardized for age by regressing each on nestling age. Residuals from these regressions were used in the subsequent analyses. Because brood size had no effect on body weight or tarsus length when included in the analyses (all $P > 0.05$), brood size was not controlled for in the analyses presented. Of the 33 nests where temperature measurements were taken, two were depredated; therefore, only 31 nests were included in the analyses testing for the strength of selection through microclimate.

Statistical analyses

To compare relative frequencies of losses through snakes, mammals and birds, and snowfall, we used χ^2-tests. Following a significant overall test, we compared differences between slope and years, separately (see Bortz *et al.* 1990).

We used two techniques to examine the effects of predation by Adders, by mammals and birds, and losses through snowfall on nest-site characteristics. To determine the strength and direction of natural selection exerted by the above-mentioned causes of nest failure on preference for nest-site characteristics, we used multiple linear regression analyses (Lande & Arnold 1983). The use of dichotomous fitness measures does not affect the estimates of the directional selection gradients (Lande & Arnold 1983), but it violates the assumptions for inference tests (e.g. Neter *et al.* 1989). Thus, we also performed logistic regressions to validate the significant effects of nest-site characteristics in the multiple regression analyses. A nest-site characteristic was considered to exert a significant effect if the full model, which included all nest-site characteristics and the intercept, was significant and the parameter estimate of the nest-site characteristics was significantly different from zero.

In both the logistic and the multiple regression analyses we assigned a fitness correlate of zero to unsuccessful nests (i.e. nests with partial or complete failure) and a fitness correlate of 1 to successful nests (i.e. nests without any losses). In the multiple regression analyses, however, we used relative values of fitness correlates (Lynch & Walsh 1998). Relative fitness is defined as the ratio of individual fitness to the mean fitness in the population. Since only successful nests contribute to the fitness in the population, the mean of the fitness correlate is the fraction of the number of successful nests. The relative fitness correlate of an unsuccessful nest is therefore zero and the relative fitness correlate of successful nests equals 1 divided by the number of successful nests.

The strength of selection exerted by the microclimate was estimated by directional selection gradients using the multiple regression approach (Lande & Arnold 1983). Relative values of fitness correlates of each nest used in these analyses were calculated as ratios of the absolute value of the fitness correlate of the nest to the mean absolute value of the fitness correlate of all nests. The absolute value of the fitness correlate for each nest was measured by four traits: number of offspring fledged, duration of nestling period, mean body weight and mean tarsus length.

All statistical analyses were performed using SYSTAT 7.01 for Windows (SPSS 1997). If not stated otherwise, means and standard deviations are shown.

RESULTS

Variation in nest-site characteristics and microclimate

Water Pipit nest cavities mainly had earth bottoms (95% of all nests) and were covered by earth (44% of all nests) or vegetation (40% of all nests), i.e. roots of shrubs. The average (± sd) relative orientation of nest cavities on the WSW slope of the valley was 7.8 ± 24.5°; on the ENE slope the corresponding values were 6.5 ± 31.3°. Average relative orientation of nest cavities did not differ between the slopes ($t = 0.426$, $df = 409$, $P = 0.670$). On both slopes, however, it differed significantly from zero (WSW slope: $t = 4.120$, $df = 169$, $P < 0.001$; ENE slope: $t = 3.235$, $df = 240$, $P < 0.002$). This means that the entrance of the nest cavity did not face in the same direction as the slope of the valley at the nest site but was slightly turned away from the slope exposition towards the entrance of the valley. The inclination of the fall line of the valley slopes at nest sites was 57 ± 20°.

The median percentage of ground cover within the 0.5-m radius samples consisted of 7% tall shrubs (min = 0%, max = 75%), 34% medium shrubs (0–97%), 14% small shrubs (0–67%), 4% ground covering vegetation (0–91%), 11% grass (1–92%), 2% bare ground (0–40%) and 2% rock (0–51%). The average rock height within this circle was 13 ± 18 cm (max: 110 cm).

The nest-site characteristics were either not correlated with each other or showed only moderate correlations (Table 1). The only exception was the strong correlation between the amount of rock

Table 1. Correlations among nest-site characteristics. Two dummy variables (dv) were used to code for the three dominating materials of bottom and cover of nest cavity.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
(1) Bottom of nest cavity – dv 1	1													
(2) Bottom of nest cavity – dv 2	−0.03	1												
(3) Cover of nest cavity – dv 1	−0.06	−0.13	1											
(4) Cover of nest cavity – dv 2	0.01	0.16	**−0.40**^{c}	1										
(5) Orientation of nest entrance	−0.06	0.01	0.02	−0.12	1									
(6) Tall dwarf shrub	0.01	−0.11	−0.03	−0.11	0.01	1								
(7) Medium-sized dwarf shrubs	0.04	0.01	0.02	−0.02	0.06	−0.08	1							
(8) Small dwarf shrubs	−0.05	−0.06	0.05	−0.08	−0.03	−0.02	**−0.38**^{c}	1						
(9) Grass	−0.09	0.02	−0.10	0.05	−0.06	−0.11	**−0.39**^{c}	**0.32**^{c}	1					
(10) Ground covering vegetation	0.15	−0.07	−0.01	0.08	0.05	**0.21**^{a}	0.08	−0.17	**−0.40**^{c}	1				
(11) Bare ground	−0.05	0.04	**0.23**^{b}	−0.13	−0.02	−0.17	0.06	−0.04	−0.08	−0.06	1			
(12) Rock	−0.09	0.06	0.01	**0.22**^{b}	−0.05	−0.12	**−0.23**^{b}	0.10	**0.23**^{b}	−0.08	0.05	1		
(13) Average height of rocks	−0.07	0.04	−0.06	**0.25**^{c}	−0.01	−0.14	**−0.24**^{b}	0.12	**0.27**^{c}	−0.10	0.02	**0.72**^{c}	1	
(14) Inclination of slope	−0.09	−0.06	**0.29**^{c}	**−0.26**^{c}	0.07	0.05	0.15	0.06	−0.15	−0.04	0.14	−0.14	−0.19	1

$^aP < 0.05$, $^bP < 0.01$, $^cP < 0.001$.

present in the surroundings of the nest and the average height of rocks. We used only one of these two highly correlated variables in subsequent analyses, because independent variables that are strongly correlated weaken multiple regression analysis through inflation of the error term (Tabachnick & Fidell 1996). Based on the finding that Water Pipits place their nests in areas with many lookout posts (Böhm & Landmann 1995), we chose to use the average height of rocks rather than the amount of rock present around the nest in the analyses, because the latter would include flat rocks that are not suitable as lookout posts.

The average (± sd) temperature minima and maxima in seven nest cavities at the WSW slope were 9.8 ± 2.9 and 15.4 ± 2.7 °C, respectively. At the ENE, slope the corresponding values for 24 nests were 8.7 ± 2.7 and 14.4 ± 2.1 °C. None of these temperatures differed between the slopes (all $P \geq 0.31$, *t*-tests). On the WSW slope temperature maxima occurred at *c.* 16 : 00 h (CET). On the ENE slope temperature maxima were measured at *c.* 10 : 00–11 : 00 h (CET). Temperature minima occurred on both slopes at *c.* 06 : 00–07 : 00 h (CET).

Relative importance of predation and snow cover

In 113 out of 325 nests (= 34.7%) at least one young was lost due to predation by Adders, predation by mammals/birds or snow cover. The relative frequencies of these three causes are plotted in Fig. 1(a). This shows that the relative importance of mortality causes decreases from mammalian and avian predation through snake predation to snowfall when nestling losses are pooled over both sides of the valley and all three years of the study, but there were clear differences in space and time (Fig. 1b,c). On the ENE slope, loss of at least one nestling occurred in 39 out of 183 nests (= 21.3%). On the WSW slope 52.1% (74 out of 142 nests) of the nests lost at least one nestling. Losses through mammalian and avian predation, and snowfall did not differ between the slopes (mammals/birds: $\chi^2 = 0.140$, $df = 1$, $P > 0.900$; snow: $\chi^2 = 0.003$, $df = 1$, $P > 0.900$, Fig. 1b). Snake predation, however, was restricted to the WSW slope, because Adders do not occur on the ENE slope (pers. obs. Fig. 1b). Snowfall caused nest failures only in 1991 (Fig. 1c). With the exception of 1992, Adder predation caused fewer losses than mammalian or avian predation (all $P < 0.001$).

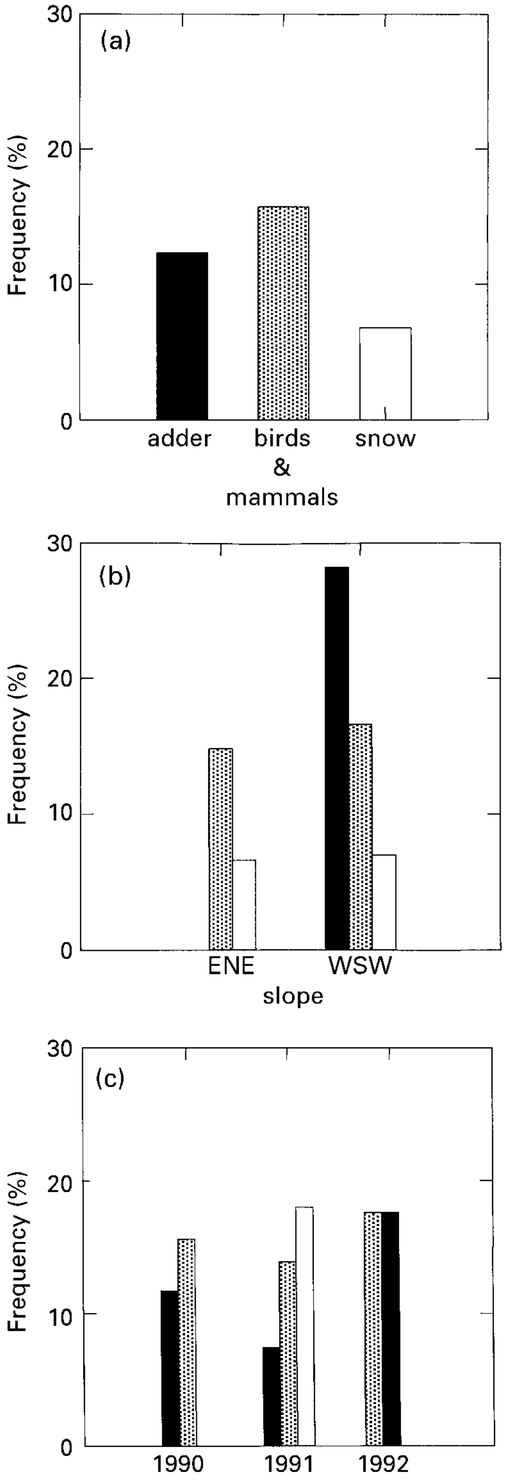

Figure 1. Relative frequencies of nestling losses or nest failure through snake predation (black bars), mammalian and avian predation (shaded bars) and snowfall (white bars). (a) Losses in relation to cause, pooled over all years and both slopes ($n = 325$). (b) Losses in relation to slopes. (c) Losses in relation to year.

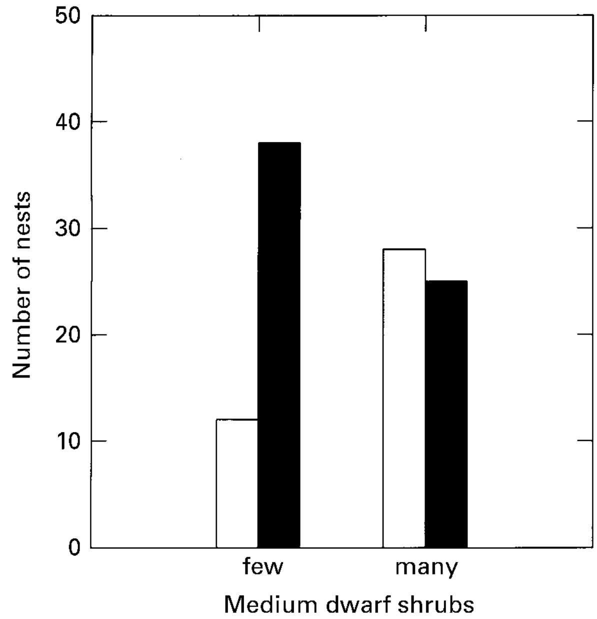

Figure 2. Number of nests predated (white bars) and not predated (black bars) by Adders in relation to the amount of medium-sized dwarf shrubs (few vs. many).

Nest-site characteristics discriminating best between successful and unsuccessful nests

With respect to Adder predation, the logistic regression analysis revealed that successful nests were characterized by vegetation containing fewer medium-sized dwarf shrubs than unsuccessful ones (Fig. 2; $\beta' = -1.325$, $P = 0.018$; β' of all other nest-site characteristics and intercept: $P > 0.132$; full model: $df = 13$, $P = 0.048$).

In terms of predation by mammals or birds none of the 11 nest-site characteristics used in the logistic regression analysis allowed discrimination between successful and unsuccessful nests (β' of all nest-site characteristics: $P > 0.085$; intercept $= 1.899$, $P = 0.017$; full model: $df = 13$, $P = 0.545$).

In the case of snowfall, the logistic regression analysis showed that few medium and short shrubs, and cavities covered with earth were characteristic of successful nests (Fig. 3; medium shrubs: $\beta' = -3.447$, $P = 0.001$; short shrubs: $\beta' = -2.283$, $P = 0.016$; earthy cavity cover: $\beta' = 1.598$, $P = 0.038$; β' of all other nest-site characteristics and intercept: $P > 0.067$; full model: $df = 13$, $P = 0.003$).

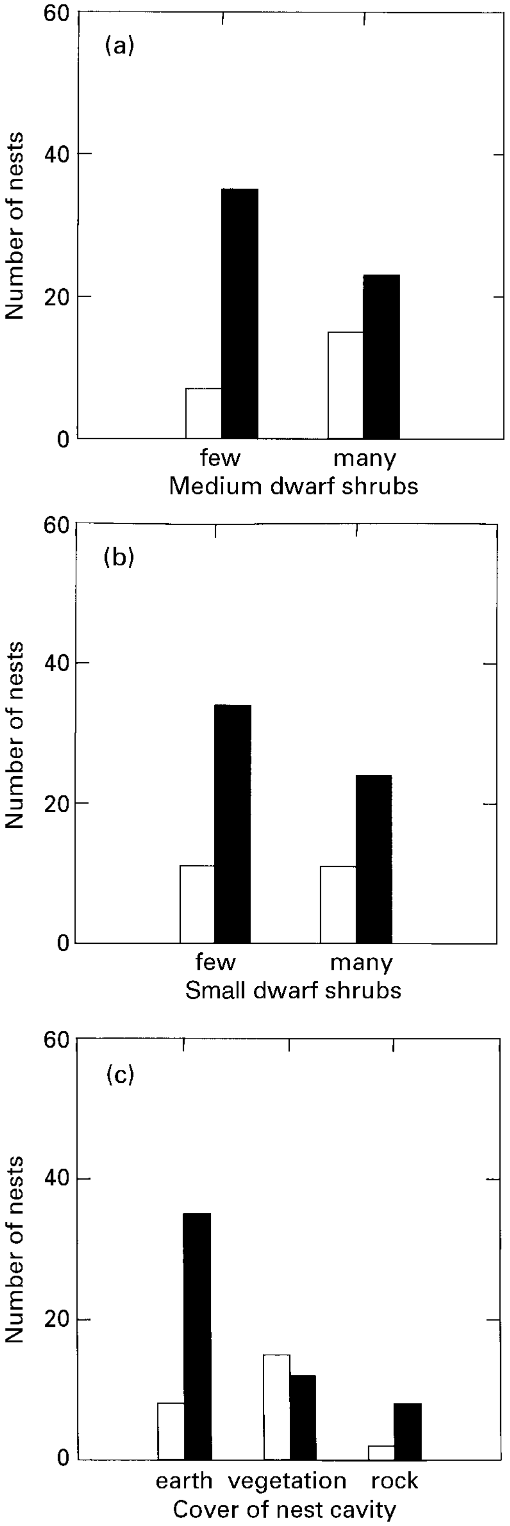

Figure 3. Number of nests that were unsuccessful (white bars) or successful (black bars) in withstanding late snowfall in relation to the amount of medium-sized dwarf shrubs (a), small dwarf shrubs (b) and cover of the nest cavity (c).

Strength of directional selection on preference for certain nest-site characteristics

With respect to predation by Adders, the only significant coefficient among the directional selection gradients was the amount of medium-sized dwarf shrub cover around the nest site ($P = 0.026$, all other nest characteristics: $P > 0.174$; intercept = 0.010, $P = 0.006$; full multiple regression model: $df = 13, 69$; $P = 0.088$). Selection by snake predation favoured nest sites with relatively few medium-sized dwarf shrubs ($\beta' = -0.004$, se = ±0.002). For natural selection exerted by mammals and birds none of the nest-site characteristics showed a significant directional selection gradient (all $P > 0.075$; intercept = 0.004, $P < 0.001$; full model: $df = 13, 241$; $P = 0.507$). With respect to late snowfall there were three significant selection gradients, increasing in importance from cover of the nest cavity to the amounts of small- and medium-sized dwarf shrubs (earthy cavity cover: $P = 0.022$; short shrubs: $P = 0.013$; tall shrubs: $P < 0.001$; all other nest-site characteristics: $P > 0.060$; intercept = 0.011, $P = 0.029$; full model: $df = 13, 66$; $P = 0.006$). Selection should favour placing nests in locations with few small- and medium-sized dwarf shrubs, and in cavities with an earthy or rock cover (earthy cavity cover: $\beta' = -0.004$, se = ±0.002; short shrubs: $\beta' = -0.005$, se = ±0.002; tall shrubs: $\beta' = 0.002$, se = ±0.002).

Directional selection gradients of thermal microclimate

Nests on the two slopes did not differ in average clutch size or in the number of hatchlings, but they did differ in the number of fledglings (Table 2). On the WSW slope, significantly fewer nestlings fledged than on the ENE slope. Although the nestling period was shorter on the WSW slope than on the ENE slope, nestlings at the age of 8–11 days did not differ in body mass and tarsus length. On the WSW slope these fitness correlates did not differ between nests with or without microclimate measurements. On the ENE slope, fitness correlates also did not differ between nests with and without microclimate measurements except for the number of fledglings and duration of nestling period. Nests with microclimate measurements showed the same nest-site characteristics as nests without microclimate measurement, except that the former had higher grass coverage in the nest surroundings than the latter (logistic regression

Table 2. Average clutch size, number of hatchlings and fledglings, duration of nestling period, and tarsus length and body mass of 8–11-day-old nestlings for nests with microclimate measurements and nests without microclimate measurements at the WSW and ENE slope. Values are mean ± se (*n*).

	Nests with microclimate measurements			Nests without microclimate measurements			+ m vs. – m	
	WSW slope		ENE slope	WSW slope		ENE slope	WSW slope	ENE slope
Clutch size	4.7 ± 0.2 (7)	n.s.	4.7 ± 0.1 (24)	4.5 ± 0.1 (131)	n.s.	4.5 ± 0.1 (159)	n.s.	n.s.
Number of hatchlings	4.7 ± 0.2 (7)	n.s.	4.5 ± 0.2 (24)	3.7 ± 0.1 (135)	n.s.	3.8 ± 0.1 (159)	n.s.	*
Number of fledglings	2.4 ± 0.8 (7)	*	4.2 ± 0.3 (24)	2.0 ± 0.2 (135)	***	3.0 ± 0.2 (159)	n.s.	**
Nestling period (days)	12.4 ± 1.0 (5)	*	14.3 ± 0.3 (24)	13.8 ± 0.2 (76)	***	14.7 ± 0.1 (121)	n.s.	n.s.
Body weight (g)	18.3 ± 0.4 (6)	n.s.	17.6 ± 0.5 (24)	18.4 ± 0.3 (66)	n.s.	18.5 ± 0.2 (86)	n.s.	n.s.
Tarsus length (mm)	20.9 ± 0.3 (6)	n.s.	19.7 ± 0.3 (24)	20.6 ± 0.1 (66)	n.s.	20.7 ± 0.2 (86)	n.s.	n.s.

n: number of nests. $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, n.s. not significant. + m vs. – m: comparison between nests with and without microclimate measurements.

– grass coverage: $b = -1.099$, $P = 0.048$; constant: $P = 0.898$; full model: $df = 13$, $P < 0.001$).

The existing differences between slopes in the number of fledglings and duration of nestling period cannot be explained by average daytime temperature maxima ($P = 0.791$ and $P = 0.438$, respectively) or average temperature minima at night ($P = 0.664$ and $P = 0.257$, respectively). However, the time of day when the temperature maximum occurred exerted significant selection on the number of young fledged ($\beta' = -0.443$, se = ±0.177, $P = 0.019$; full regression model: $df = 3, 27$; $P = 0.085$) and the duration of the nestling period ($\beta' = -0.149$, se = ±0.058, $P = 0.016$, full regression model: $df = 3, 24$; $P = 0.077$), but not on the quality of the offspring in terms of size and weight (both $P > 0.572$). Nests with the maximum temperature in the morning (i.e. on the ENE slope) fledged more young than nests where the maximum temperature occurred in the afternoon (i.e. on the WSW slope; Fig. 4a). The nestling period was shorter for nests with maximum temperature in the afternoon (Fig. 4b).

Food availability and feeding rates

Prey sampling in 1991 and 1992 showed that the two slopes also differed in food availability. Averaged over both years, mean (± se) prey biomass was 3.1 times higher on the WSW than on the ENE slope (27.8 ± 3.6 vs. 9.0 ± 1.0 mg dry weight per sample; $t = 12.1$, $df = 262.7$, $P < 0.001$). Nevertheless, mean feeding rates per hour did not differ between the two slopes (12.6 ± 2.0 vs. 10.3 ± 0.6; ANOVA: $F_{1,22} = 0.847$, $P = 0.367$) but varied with number of nestlings and ambient temperature (both $F_{1,22} > 8.5$, both $P < 0.008$).

DISCUSSION

We found weak, but significant, directional selection on nest-site characteristics and, hence, selection on preference for specific nest-site characteristics in Water Pipits. Predation by Adders selected for nest sites surrounded by few medium-sized dwarf shrubs. This result might reflect avoidance by Adders of this particular microhabitat, rather than a reduction of predation risk through the vegetation structure. Some snakes concentrate their foraging activity in specific habitats (Weatherhead & Charland 1985). One reason may be that the structural complexity of the vegetation affects their overall foraging success (Mullin *et al.* 1998). Within their preferred habitat,

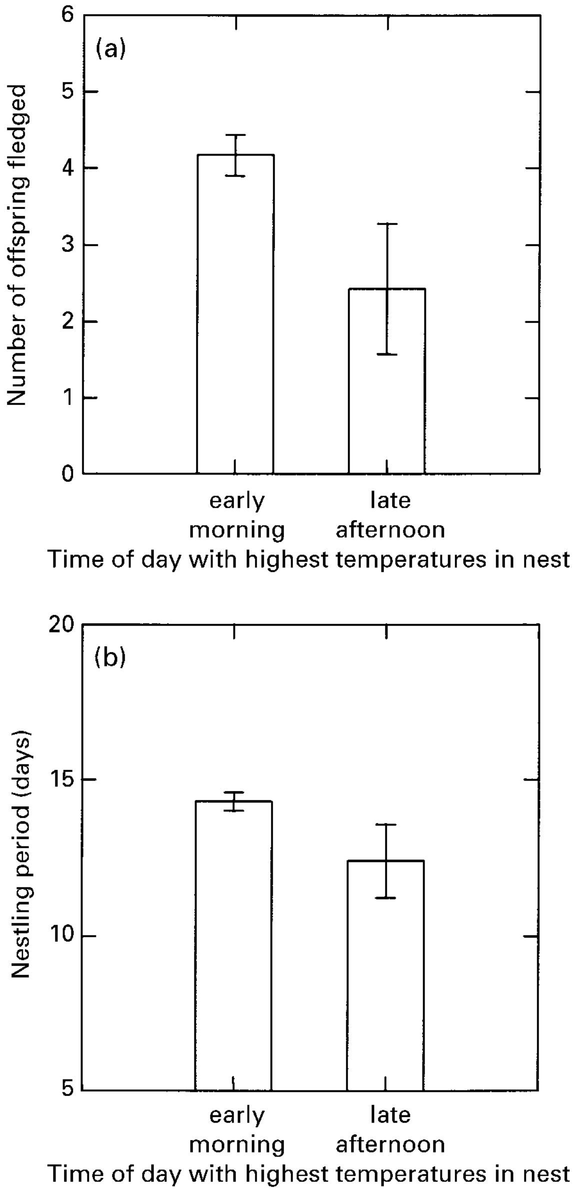

Figure 4. Number of fledglings (a) and duration of nestling period (b) in relation to time of day when maximum temperatures occurred. Means and standard errors are shown.

however, snakes seem to forage randomly, and nest concealment does not seem to reduce snake predation (Best 1978). This could result from the fact that snakes use not only visual, but also olfactory, cues to locate prey (e.g. Ashton & Ashton 1981, Mullin *et al.* 1998). An alternative explanation for possible snake concentrations is that a particular vegetation type may hold higher densities of prey. Such a density-dependent response has been reported for other systems of snake/bird predation (e.g. Best 1978). For our study area, however, we have information about neither the spatial distribution of Adders nor of their prey, which includes not only nestlings of various bird species but also mice, voles and lizards (Neumeyer 1984).

Selection by mammalian and avian predators favoured no specific nest-site characteristics. Since 44 of the 51 nest losses in this predation category were due to mammals, our results support the finding by Clark and Nudds (1991) that nest concealment is less effective against mammalian predators with good olfactory senses.

Protection from snowfall was not clearly related to a single nest-site characteristic but to a complex combination of vegetation and cavity material features. Protection was better in nests surrounded by relatively few medium-sized and small dwarf shrubs, and with a cavity cover of earth or rock rather than vegetation. This difference may result from the fact that vegetation can collapse under the weight of snow and, thus, bury the nest or prevent parents from getting access to the young.

In terms of nestling development, there was strong selection exerted by the time of day when maximum temperatures occurred. Nests with temperature highs in the morning fledged more young than those with highs in the afternoon (based on unpredated nests alone). The diurnal temperature pattern was, however, confounded by the slope of the valley; nests with maximum temperatures in the morning were located on the ENE slope and nests with maximum temperatures in the afternoon were located on the WSW slope. Based on food availability, we would have expected higher nestling survival on the WSW slope, because here mean prey biomass measured by sweep-netting was higher than at the ENE slope. The fact that the reverse was true indicates that the survival of the nestlings was probably directly affected by the microclimate they experienced.

On the ENE slope, nests might profit from the warming morning sun which would dry the dew damped nest material and allow the parent bird to stay longer away from the nest foraging to compensate for overnight energy expenditure. As the morning sun is not as intense as in the afternoon, the risk that nestlings overheat is low. Heat stress can, however, pose a problem on the WSW slope, especially in the afternoon. On sunny days panting or lethargic nestlings, stretching their heads to the shadiest area of the nest, were observed only on the WSW slope, but never on the ENE slope. In ground-nesting birds, heat stress, due to intense sunlight, can kill nestlings

(Salzman 1982, Murphy 1983) or force them to leave the nest earlier than under favourable microclimatic conditions because the vegetation close to the nest provides more shade and protection from the heat (Hötker 1990). This would explain why the nestling period on the WSW slope is shorter than on the ENE slope.

An alternative to the 'thermal hypothesis' above is based on the difference in predation rates between the slopes. The higher predation rate on the WSW slope may result in higher vigilance of the parents there, compared with those on the ENE slope. Since vigilance and foraging are conflicting behaviours, birds on the WSW slope should devote less time to foraging and feeding their young than birds on the ENE slope, with the consequent differences in fledgling production. However, this explanation seems unlikely because feeding rates did not differ between the slopes.

Our results from Water Pipits indicate that natural selection should drive a preference for certain nest-site characteristics through its effects on survival and nestling development. Whether this selection translates into the evolution of choice of specific nest sites remains an open question because there are no data available on heritability of nest placement for this or any other bird species. In some species, offspring tend to prefer the same type of nest site as their parents (Pinkowski 1979, Herlugson 1981). Although heritability is one possible reason for this consistency in nest placement, familiarity with this nest type through learning cannot be excluded as an explanation. Moreover, even if there is evolution, its speed and direction is difficult to tell because selection varies in space and time. For example, placing nests under shrubs may be favoured by microclimate because it reduces heat stress, but it may be selected against through predation by Adders which is higher in bushy areas. Hence, the best strategy will depend on the relative importance of these events which, in turn, can differ between areas (e.g. slopes) and years (cf. Fig. 1). Since nestling loss due to predation and snowfall seems to be fairly unpredictable within a particular area like the WSW slope (Bollmann *et al.* 1997), there may be little scope for the evolution of an optimal nest placement strategy on a small scale, and flexible rules of nest placement would be more appropriate. On a larger scale, however, choice of one breeding area over another may be favoured because there are predictable differences between locations (here WSW vs. ENE slope) in terms of survival and nestling development.

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