

TERRITORY QUALITY AND REPRODUCTIVE SUCCESS: CAN WATER PIPITS *ANTHUS SPINOLETTA* ASSESS THE RELATIONSHIP RELIABLY?

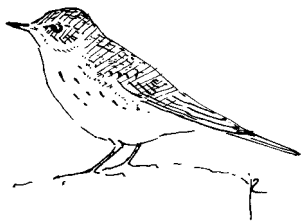
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Variation in avian reproductive success is often caused by differences among territories in food supply, safety from predators and microclimatic conditions at the nest. Yet, in some habitats these components of territory quality, and hence future reproductive success, are difficult to assess at the time of settlement. Here, we analyse territory quality for Water Pipits breeding in an unpredictable alpine habitat and relate it to settlement patterns and reproductive success. In the study area, prey biomass differed between various vegetation types and steadily increased during the breeding season. Territory-specific prey biomass was negatively correlated to snow cover during the pre-breeding period. Males, on average, arrived prior to ♀♀, and both sexes settled earlier in prey-rich than in prey-poor areas. Early settling ♂♂ also occupied larger territories, early settling ♀♀ showed a longer time lag between settlement and clutch initiation than late ones. However, prey biomass, territory size and time lag as well as male and female age were not related to clutch size and number of fledglings per brood and season. The only factor significantly determining reproductive success was the occurrence of nest predation for which we could not find an environmental predictor. Apparently, the birds could not either, because both sexes settled independent of later predation. In the discussion we address the question why Water Pipits cannot reliably assess habitat quality when choosing a territory and what alternatives they have.

Key words: *Anthus spinoletta* - habitat selection - breeding success - territoriality - predation - assessment processes - information - passerines

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INTRODUCTION

Territoriality is a common feature among land birds; 84% of the passerines and 81% of the non-passerines breed in territories (Lack 1968). For ♂♂, resource defence through territorial exclusion of competitors is usually a precondition for obtaining mates, and reproductive success of both sexes may increase with territory size and/or quality (Verner & Willson 1966, Davies 1991, Goodburn 1991). Ens *et al.* (1992) listed the evidence from various studies that allow to infer the exist-

tence of differences in territory quality. In long-term studies mainly three factors turned out to be good quality measures related to reproductive success. First, the amount and quality of food is often a critical resource determining the fitness of animals (reviewed by Martin 1987), especially in species where the majority of feeding is done within the territory (Högstedt 1980). Second, protection from nest predation influences breeding success (e.g. Holm 1973, Weatherhead & Robertson 1977, Askenmo & Neergaard 1990). Third, microclimatically advantageous nest sites may be a lim-

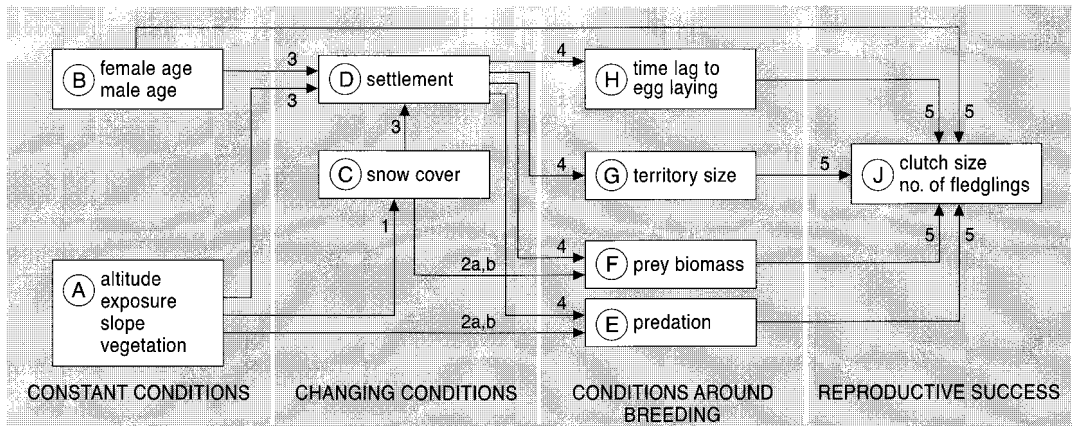


Fig. 1. Path diagram illustrating potential connections between ecological and phenotypic features that remain constant during the breeding season (A, B), those that change in time (C, D), conditions around breeding (E-H) and various measures of reproductive success (J). The numbers correspond to the statistical analyses in the successive 'Results'-sections.

iting resource and contribute to variation in reproductive success (e.g. Ligon & Ligon 1988 & 1989). Therefore, it would be advantageous to settle in high quality areas. However, in many areas only a limited amount of environmental information is available during the period of arrival and birds have to use proximate factors as clues to assess territory quality and the potential for reproduction.

Alpine habitats are typical for such areas. The amount of snow accumulated over winter and the rate of snow melt in spring determine when bare ground becomes visible (Smith & Andersen 1985). As a consequence, environmental conditions at the start of the breeding season can differ markedly from year to year, and birds arriving in their breeding area may find it still completely snow covered. In such years, they cannot base their choice of territory on a direct appraisal of food supply, protection from predators, microclimate at the nest site, or other measures of quality. Adults that know the area from previous breeding attempts may use their experience; but first time breeders must assess territory quality solely by the information available at the time of their arrival. Once a breeding territory has been chosen, later boundary change or switch may be difficult

(Davies & Houston 1984). The alternative to establish his territory later, when more reliable cues are available, may be costly for a young σ since he may be forced to settle in poor habitat, fail to get a mate and forego the chance of successful reproduction. It has been demonstrated in many species that being present at a site for some time prior to a social interaction increases status, and this advantage can outweigh other determinants of dominance (e.g. Cristol *et al.* 1990).

The Water Pipit (*Anthus spinoletta*) is a short-distant migratory, obligate ground-nesting, short-lived, insectivorous passerine with a resource-defence territory system. Birds return to their breeding grounds in spring, usually from the end of April to mid-May, and establish territories when the area is still snow covered. During this period, on fine days, the first $\sigma\sigma$ fly to these grounds and intensively defend territories for some hours in the morning before they return to foraging and sleeping places in lower areas of the valley (Catzeflis 1978, Biber 1982, this study). The costs of this back-and-forth movement in terms of time and energy must be outweighed by the benefits of early territory ownership for subsequent mating chances and breeding success. When snow melting lays bare the first patches of vegetation more

♂♂ arrive and settle along. As climatic and habitat conditions improve, birds stay continuously in their breeding territories and usually do not leave them in the evening any more; but even at this time, spring snowfalls occasionally force them to abandon their territories and to descend to lower areas for some days.

In this paper, we attempt to relate reproductive success to three measures of territory quality that cannot reliably be assessed early in the breeding season, namely food supply, availability of safe nests and microclimate at the nest site. The rationale of our approach and the sequence of the various analyses is illustrated in Fig. 1. In analyses 1-4, we investigate the links between conditions that are constant throughout the season and can be perceived upon arrival (A and B in Fig. 1), conditions changing with time (C, D) and those prevailing around breeding (E-H). In analysis 5, we relate reproductive success (J) to those breeding conditions (E-H) and to phenotypic traits of the breeders (B). In the discussion, we address the relevance of the various quality measures as potential criteria for territory choice.

METHODS

Territorial and foraging behaviour

A comprehensive description of the Water Pipit behaviour is given in Glutz von Blotzheim & Bauer (1985) and Cramp (1988). Territory establishment is exclusively done by the ♂♂. During the period of settlement and pairing they mark the territory with flight-songs, alert-postures and display patterns. Contests at the boundary are often performed as parallel-walk display with tail raised and wings drooped and subsequent air chases. Sometimes they also perform violent fights on the ground and in the air. For their conspicuous flight songs, ♂♂ start from the top of a bush, a rock or another sentinel point and ascend until they have reached the summit of their flight. Thereafter they descend and delimit the territory by circling and traversing from boundary to boundary before landing. A variant of the flight-song is often performed along the territory boundaries by flying from bush to bush or from rock to rock. The territory system is very stable at this time of the season (Askenmo *et al.* 1994, own observations).

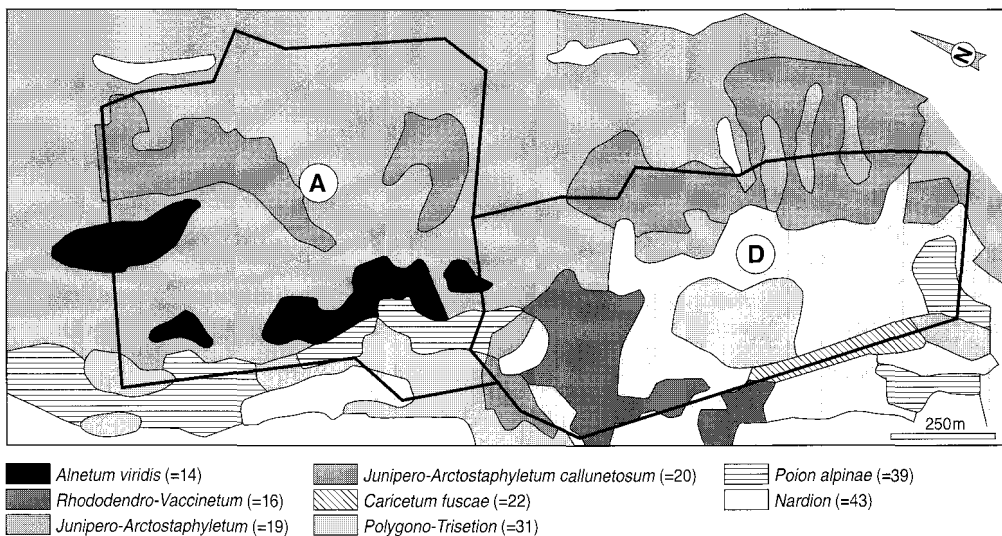


Fig. 2. Vegetation map of the study site after Zumbühl & Burnand (1986). The study area (within the thick line) was divided into two connected plots A and D.

The Water Pipit's principal foraging technique involves continuous walking on the ground or climbing through shrubs and picking diurnally available invertebrates, mainly arthropods, from the ground and vegetation. Occasionally it catches insects in flight by making short leaps or flying from perches. Food provided to nestlings is mainly composed of five prey taxa (78% of biomass; Brodmann *et al.* 1997b). In decreasing order these taxa are Leptidoptera larvae, Tipulidae (Diptera), Araneae, Saltatoria and Rhagionidae (Diptera).

Study area, ecological conditions and breeding periods

The study was carried out from 1990–1993 in the northern continental zone of the central Alps in the valley of Dischma (46°06'N, 09°53'E) near Davos, Kt. Graubünden, Switzerland. The study area of 1.5 km² lies in the upper, forest free part of the valley at elevations between 1830 and 2300 m.s.l. It is mainly exposed to south-west, with slopes ranging from 0 to 50° ($x \pm SD$: $23 \pm 12.0^\circ$). Details about the weather and climate of the study area are found in Bollmann (1996). The vegetation of the valley has been mapped prior to this study by plant sociologists during the international research program 'Man and Biosphere MAB' (Zumbühl & Burnand 1986). According to them eight vegetation units are found in the study area (Appendix A). They can be classified as five vegetation types by their composition and management practice: (1) subalpine meadows and pastures (22, 31, 39, 43); (2) medium sized dwarf shrub dominated by *Calluna* (20); (3) large sized dwarf shrub dominated by *Rhododendron* (16); (4) large sized dwarf shrub dominated by *Juniperus* and *Vaccinium* (19); (5) large sized dwarf shrub dominated by *Alnus* and *Betula* (14).

These five vegetation types increase in height and prey biomass. Type 5 differs from type 4 only by the presence of scattered *Alnus* and *Betula* bushes, the ground vegetation is equal. Since no prey sampling was practicable in vegetation type 5, its prey biomass was equated with that of type 4. We think that this procedure is justifiable

especially because Water Pipits foraged exclusively in the ground vegetation and only two territories were partially covered by type 5 vegetation. Dwarf shrubs and pastures are stocked by cattle and cows in summer, meadows are used for hay production. Figure 2 represents a map of the study area with its main vegetation units and the two connected study plots A and D. The former lies in the direction of the valley opening and is less extensively managed by men than plot D.

A 50 × 50 m grid system was put over a topographical map of the study area (scale 1 : 5000). For the centre of each 0.25 ha square the following ecological parameter were recorded from the map: altitude, gradient and compass direction of slope, main vegetation unit (the one out of eight vegetation units with highest percentage of cover in a specific grid) and snow cover. To measure the latter, the study area was documented by panorama-photos every six to ten days. From the pictures areas with snow were drawn onto the topographical map. Thereafter, grid and territory specific snow patterns could be ascertained with an accuracy of 5%.

Available food supply was sampled by one person in a standardized way with a sweep net, the best of five originally tested methods (Brodmann 1995). Throughout the breeding season, prey sampling was done every second week, on fine days, in about 30% of the grid squares. These represented each vegetation unit and altitude in proportion of their occurrence. The sum of the nine prey taxa which are most important as nestling food was used as an estimate of the total biomass of available prey of a grid square. Each of the nine taxa accounted for at least 1% and all taxa together amounted to 88.8% of the prey biomass fed to the nestlings (Brodmann *et al.* 1997b). So, we were able to calculate an average prey biomass density (mg drymass per sample) – hereafter referred to as prey biomass – for each vegetation unit and sampling by summarizing the data of all grids of a specific unit. For the analyses we split the prey sampling data into two periods, each containing two sampling dates: 3–21 June and 14–30 July. These periods coincided well with the

first breeding period (FBP) and the late breeding period (LBP), respectively. The FBP comprised all first breeding attempts in a season, the LBP included replacement clutches and second breeding attempts. We speak of a breeding attempt when the nest of a ♀ receives at least one egg. Hatching during the FBP and LBP took place from 5–25 June and from 7–24 July, respectively. The average prey biomass was calculated separately for both periods and each of the eight vegetation units. Based on the proportion of the various vegetations in a territory, these vegetation-specific prey biomasses were then used to calculate territory-specific prey biomass. Further details about prey sampling are given by Brodmann *et al.* (1997b).

Behavioural observations and reproductive success

The Water Pipit population was studied from 1990–1993, but with different emphasis in different years. The complete data set required for the subject of this paper was collected in 1992 only. At the beginning of the breeding season, 52% of the ♂♂ and 41% of the ♀♀ that performed a breeding attempt during the FBP ($n = 39$) were individually colour-ringed. Since some birds had been born before the study began, the ages used in the analyses refer to minimum ages. Unbanded breeding adults that settled in the study area were considered to be one year old. Justification for this assumption is given by Bollmann (1996).

Observations started on 22 April which is about the time the first individuals arrived. On 15 April no Water Pipits had arrived in the study area yet. Settlement date refers to the first day a ♂ was observed on the ground where he subsequently showed territorial behaviour or to the first day a ♀ was observed on the territory where she subsequently built her first nest. For unbanded birds, we considered consistent sighting of an individual on a territory as evidence that the individual was always the same. From settlement of the first birds throughout the breeding season observations were made on average six days per week. Each part of the study area was checked for indi-

viduals every third or fourth day. Daily observation were conducted from dawn to 13.00 h and from 17.00 h to dusk. After the first nests had been initiated, evening observation were combined with nest controls. In order to determine the territory and the mating status of ♂♂ and ♀♀, during each visit the presence or absence of territorial (see above), courtship and nest oriented behaviour of all individuals were recorded on a map (scale 1: 2500). Each day these data were analysed and the actual territory pattern map and status of each individual was used for subsequent nest search. Territory size and shape was determined by the minimum concave polygon method (Clutton-Brock *et al.* 1982) based on the typical observation points of ♂♂. These included starting and landing points of song-flights, perches of lookout posts, sites of ♂-♂ displays and fights as well as locations of courtship flights and regular feeding activity. The estimate of territory size increased with the observation time and the number of registrations. At least 45 minutes of continuous observation time were needed to reach asymptotic size estimates. In this paper territory shape and size refer to the males' territories during the pre-breeding period. For paired ♂♂ this is the period from settlement until completion of the clutch, for bachelors from settlement until 1 June which was the median clutch completion date of the FBP in 1992. For analyses using variables with an area component (e.g. territory size, snow cover), only data from those pairs were used that reached the minimum registration of 45 minutes on at least three different days during the pre-breeding season ($n = 39$). In the absence of confirmed breeding, a territory was assumed to be occupied if a ♂ or a pair was present during at least 50% of three or more visits to the territory area before the median clutch completion date. The ascertainment of territory site, shape and size was done with a CAD-software (Grafsoft 1992). For each territory we calculated the proportion of each vegetation unit and determined the main vegetation type, i.e. vegetation type with highest percentage within a single territory.

A home range refers to the range used by a

pair for resting, foraging and breeding behaviour during the first breeding attempt (completion of the clutch until fledging of young). It includes areas within the own and in neighbouring territories. Both, territories and home ranges exclude occasional feeding trips to distant communal feeding sites (meadows, little swamps).

A big attempt was made to find the well-hidden nests as early as possible. They were detected in different ways: by watching nest building ♀♀, by watching ♀♀ returning to the nest after a foraging trip, or by watching parents when feeding nestlings. In 1992 out of 49 first breeding attempts 83.7% could be detected during the nest building, laying or breeding period; the rest was discovered during the nestling period. Since we knew the nests of all territorial pairs in the FBP we estimate that at least 90% of nests in the study area were detected. Nests were marked by a 50–60 cm long bamboo stick placed in a distance of two meters from the nest entrance. It allowed to quickly find the nests again, without enhancing predation risk by directly marking them. We monitored nests every 2–4 days, depending on the breeding stage, and daily when hatching or fledging could be expected. In this way the causes of nestling mortality could be ascertained in most cases. In cases where nests were found after laying or hatching, clutch initiation (hereafter referred to as laying date) was determined by back-dating. Calculations were done by determining nestling age on the basis of morphological measurements and by assuming that the incubation lasted 15 days, incubation started with the last egg, and the laying interval was 24 h (Bollmann 1996).

Clutch size refers to the number of eggs in a nest. For nests that were found after hatching the number of nestlings was assumed to represent the original clutch size, since nests found before and after hatching did not differ in the number of eggs or nestlings, respectively (Bollmann 1996). Number fledged refers to the number of nestlings that reached banding age (7–10 days) and were not found dead in or near the nest at fledging age (10–18 days), provided there was no evidence of nest predation at the particular nest. A breeding

attempt was considered successful when at least one young fledged. Annual reproductive success describes a pair's total number of young fledged during the breeding season.

Statistics

For territories in hilly terrain a two-dimensional projection of territory size (s) onto a map produces a measure that differs from the real territory size (s^*). The same is true for vegetation cover and other area-related data taken from topographical maps. Therefore we corrected such data with the following equation: $s^* = s/\cos\alpha$. Here, α is the slope of the hillside within a territory calculated from the projection of the fall-line through the centre of each territory (x) and the difference in elevation between its two cross-points with the territory border (y). The quotient y/x defines the tangent of the slope. In analogy we corrected the size of each grid to ascertain real measures of the study area, vegetation and snow cover.

Statistics were calculated with JMP 3.0.2 (SAS Institute 1994) and SYSTAT 6.0 for Windows (SPSS Inc. 1996). Prior to analysis altitude and territory size were log-transformed, slope and snow cover arcsin-sqrt-transformed. Non-parametric statistics was used where requirements for parametric tests were not fulfilled. Estimates of errors are standard errors unless otherwise stated. Pairwise comparisons are two-tailed.

RESULTS

Ecological correlates of microclimate (snow cover)

In the Dischma valley the snow melting pattern differed distinctly from year to year. At the time of the birds' arrival, the amount of snow cover ranged from about 10–15% in 1991 through 50% in 1990 to 90–100% in 1992 and 1993. For the following description and analysis we only consider the situation in 1992. With the exception of the cliffs and a 1.5 ha vegetation patch that became snow free through an avalanche, the study site was completely snow covered at the time of

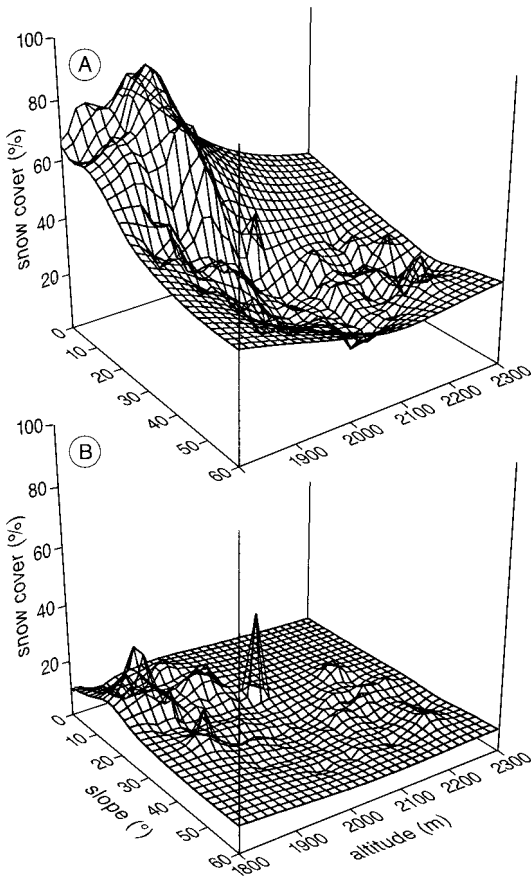


Fig. 3. Surface plot relating the amount of snow cover (%) on (A) May 19 and (B) May 28, 1992 to altitude (m.s.l.) and slope of the hillside (°) for 488 squares of 50 × 50 m each. The surface was produced with SYSTAT 6.0, using the INVERSE smoothing method with a tension of 0.2. Note that in (A) steep medium and high altitude areas have less snow than low altitude areas in and near the valley bottom. This relationship gets lost within the process of snow melting (B).

the first territory establishment in this year.

A multiple regression analysis (path 1 in Fig. 1) relating snow cover (C) on 19 May – one day after the first egg in the population was laid – to altitude, exposure, slope and vegetation (A) revealed that snow cover decreased with increasing slope ($P < 0.001$) and was affected by the vegetation type ($P < 0.001$), while altitude ($P = 0.65$)

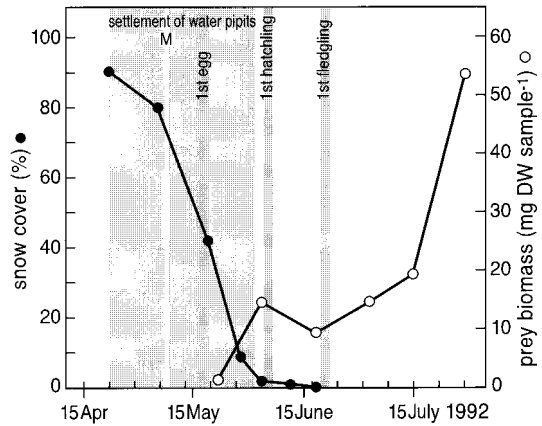


Fig. 4. Phenology of snow melting (dots) and prey biomass (open circles; mg dryweight per sample) in 1992, pooled over all vegetation types in the study area. In addition, the settlement period of birds and some key dates of breeding are indicated. M: median date of settlement.

and exposure ($P = 0.80$) had no effect on snow melting (ANCOVA; $F_{6,481} = 100.13$, $P < 0.001$). The interesting point to note is that steep areas medium and high altitudes, mainly covered by vegetation types 2, 4 and 5, had less snow than flat areas at low altitudes, including those near the valley bottom, where vegetation types 1 and 3 are concentrated (Fig. 3A). This relationship diminished within the process of snow melting (Fig. 3B).

Ecological correlates of prey biomass and predation

The ecological conditions and site management practice of an area result in different vegetation types (Fig. 2, Appendix A) and these influence insect distribution, phenology and abundance. An ANCOVA (path 2a in Fig. 1) relating territory-specific prey biomass (F) to altitude, exposure, slope, vegetation (A) and snow cover (C) on May 19 gives a significant result ($F_{7,31} = 63.93$, $P < 0.001$). Prey biomass decreased with snow cover ($P = 0.026$) and was related to the main vegetation of a territory ($P < 0.001$). Areas with dwarf shrub (2, 3, 4) had consistently higher

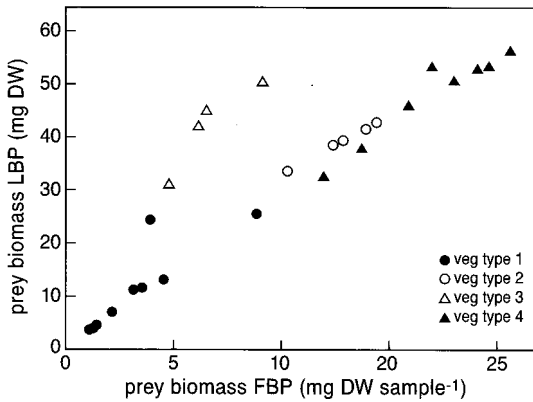


Fig. 5. Relationship between territory-specific prey density indices (mg dryweight per sample) during the first (FBP) and the late breeding period (LBP) for territories in different vegetation types (veg type).

prey biomass than areas with meadows and pastures (1), both over the whole season and for FBP and LBP separated (Table 1). Because of these significant differences, the four vegetation types are occasionally only separated into prey-poor (1) and prey-rich (2, 3, 4).

In general there was a steady increase of available prey biomass during the breeding season (Fig. 4). Overall, average prey biomass was four times higher during the late than in the first breeding period (Wilcoxon two-sample test; $Z = 4.30$, $P < 0.001$, $n = 170$), but territory-specific biomasses during the two periods were highly correlated (Fig. 5; $r_{46} = 0.97$, $P < 0.001$). Thus, prey levels of one site or territory early in the season seemed to be good predictors of later prey availability at the same site. Considering the relationship between prey density and vegetation described above, this finding is to be expected. An interannual comparison showed no difference in the general pattern of vegetation-related prey abundance and composition, but phenology did shift in time between years due to different weather regimes (Brodmann unpubl. data). This is consistent with the snow-prey relationship that we found.

Fifty-six percent of all first brood attempts ($n = 39$) were predated by Adders *Vipera berus*, Red Foxes *Vulpes vulpes*, Stoats *Mustela erminea* and Carrion Crows *Corvus corone* in decreasing order. The amount of loss depended on the age of the clutch when predation took place. During the

Table 1. Comparison of prey biomass (mg drymass per sample) of the various vegetation types for two different breeding periods (two prey samplings each) and the whole breeding season (six prey samplings) of 1992. Vegetation types: 1: meadows and pastures, 2: medium sized dwarf shrub dominated by *Calluna*, 3: large sized dwarf shrub dominated by *Rhododendron*, 4: large sized dwarf shrub dominated by *Juniperus* and *Vaccinium*. Data given are means \pm 1 SE, sample sizes in parenthesis. Significance levels: *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$. Kruskal-Wallis one-way ANOVA: First breeding period, U-tests: 1 vs. 2, **; 1 vs. 3, ***; 1 vs. 4, ***; 2 vs. 3, **; 2 vs. 4, N.S.; 3 vs. 4, N.S. ($P = 0.06$). Late breeding period, U-tests: 1 vs. 2, *; 1 vs. 3, ***; 1 vs. 4, *; 2 vs. 3, N.S.; 2 vs. 4, N.S.; 3 vs. 4, N.S.

Type	Breeding period					
	First		Late		Overall	
	$\bar{x} \pm SD$	<i>n</i>	$\bar{x} \pm SD$	<i>n</i>	$\bar{x} \pm SD$	<i>n</i>
1	1.24 \pm 1.73	62	4.09 \pm 11.49	10	1.57 \pm 2.59	75
2	10.31 \pm 3.52	15	33.49 \pm 14.83	6	14.18 \pm 4.39	26
3	7.94 \pm 4.55	9	55.08 \pm 25.59	2	18.42 \pm 6.47	12
4	20.74 \pm 1.93	50	56.07 \pm 9.08	16	26.38 \pm 2.50	80
<i>H</i>	73.793***		15.807**		79.617***	

first ten nestling days, predation generally caused loss of the whole brood (68%) whereas later on losses could also be partial and depended on the predator species.

To test whether birds could use environmental cues during settlement to assess the safety of a nest site we related the occurrence of nest predation (E) during the breeding season to the constant (A) and changing (C) environmental conditions of a territory (path 2b in Fig. 1). The overall model missed significance (logistic regression: $\chi^2_7 = 13.40$, $P = 0.063$, $n = 39$), suggesting that the set of variables considered does not allow $\sigma\sigma$ to assess predator activity accurately at the time when territory boundaries are fixed but most Adders are still in hibernation. Familiarity with an area, however, can probably influence a male's settlement. There was a decrease of nest predation with male age ($\chi^2_2 = 10.23$, $P = 0.037$, $n = 39$). Predation rates at nests of one, two and three year old $\sigma\sigma$ were 72.7, 54.6 and 0.0%, respectively ($n = 22$, 11, and 6).

Settlement in relation to phenotypic and ecological conditions

In this section we investigate how the constant (A) and seasonally changing environmental conditions (C) analysed above, together with two phenotypic traits (sex, age; B), affect the settlement (D) of the arriving birds (path 3 in Fig. 1). We will consider data from the whole population when analysing the temporal pattern of settlement. For analyses involving spatial measures (e.g. snow and vegetation cover) we will consider only pairs or bachelors for which we have the minimum number of observations required for reliable territory size estimates (see 'Methods'). Therefore, not all relationships can be tested in one analysis and sample sizes can slightly differ between analyses.

The date of settlement was significantly related to both phenotypic and ecological conditions (Table 2). In terms of phenotype, sex but not age had an effect on arrival. Males settled between the 22 April and 1 June 1992 (mean 6 May, $n = 56$). Females arrived on average three days la-

Table 2. Summary statistics of an ANCOVA for settlement of Water Pipits in relation to phenotypic and ecological variables. Prior to the analysis altitude was log-transformed, snow cover and slope were arcsin-sqrt-transformed.

Source	SS	df	F	P
Sex	170.328	1	8.351	0.005
Age	15.872	1	0.778	0.381
Snow cover	46.163	1	2.263	0.137
Altitude	6.415	1	0.315	0.577
Exposure	9.641	1	0.473	0.494
Slope	40.488	1	1.985	0.164
Vegetation	161.665	3	2.642	0.057
Error	1305.302	64		
Model	755.577	9	4.116	0.001

ter (range: 24 April–25 May, $n = 40$). In terms of ecology, vegetation of a territory seems to determine the settlement date of the birds. The effect is only marginally significant ($P = 0.057$) when we treat the four vegetation types separately; but when we only distinguish between prey-poor grass (type 1) and prey-rich shrub vegetation (types 2-4; cf. Appendix A) it is obvious that the latter is settled earlier ($P = 0.016$).

Effects of settlement date on mating and breeding conditions

For examining the effects of male and female settlement patterns on mating chances, laying date and conditions around breeding (path 4 in Fig. 1) we considered only data from Water Pipits paired during the first breeding attempt. Prey-rich areas were settled earlier than prey-poor areas by both, $\sigma\sigma$ and $\varphi\varphi$ (Table 3). This is consistent with the result that shrub vegetation is occupied earlier than grass vegetation (see above and Table 1). Female settlement date also affected the time lag between until egg laying. Late arriving $\varphi\varphi$ initiated clutches about one to two weeks after pair formation, whereas early $\varphi\varphi$ waited up to four weeks. In all study years, early pairs were forced by late snow falls in spring to leave their territories and descend down-valley for several

Table 3. Spearman rank correlation coefficients of male and female settlement in relation to variables describing conditions around clutch initiation (time lag: time between arrival and settlement). Significant probabilities are two-tailed: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, others $P > 0.05$.

Variables:	♂ settlement		♀ settlement	
	<i>n</i>	r_s	<i>n</i>	r_s
Territory size	37	-0.388 **	33	-0.123
Time lag	33	-0.226	33	-0.583 ***
Prey biomass	37	-0.389 **	33	-0.359 *
Predation	37	-0.244	33	0.133

days. Male settlement was further related to territory size. Early settling ♂♂ defended bigger territories. During the FBP seven (15%) out of 46 ♂♂ remained bachelors. Their territories had an average size of 1.12 ± 0.12 ha ($n = 7$) compared to 1.51 ± 0.28 ha ($n = 39$) of mated ♂♂. Although the difference was not significant (Wilcoxon two-sample test; $Z = -1.28$, $P = 0.20$), a male's probability of becoming paired tended to increase with the size of his territory (logistic regression: $\chi^2_1 = 3.08$, $P = 0.079$, $n = 46$).

Territory boundaries and sizes were rather stable during a breeding season, but home ranges during foraging could deviate from territory areas. This deviation was related to the territory-specific prey biomass: pairs in prey-rich territories restricted their range more than pairs of prey-poor territories (Fig. 6). On average, home ranges were 33% smaller than territories and more pairs restricted their foraging to parts of their territories compared to pairs that extended it beyond their territory boundaries (χ^2 : $\chi^2_1 = 7.53$, $P < 0.01$, $n = 34$).

Reproductive success in relation to phenotypic and ecological conditions

Considering reproductive success (J) of first breeding attempts only, the phenotypic (B) and ecological factors (E-H) under consideration (path 5 in Fig.1) could not explain the variation in

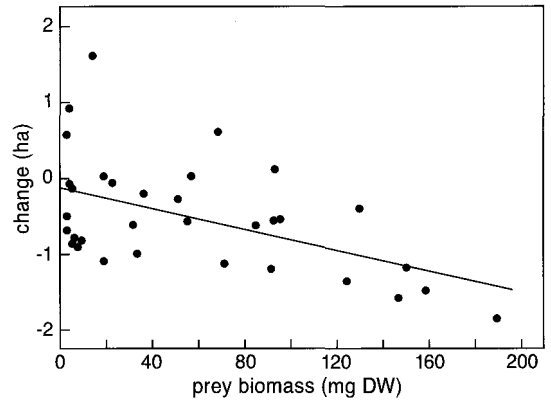


Fig. 6. Change in territory use in relation to territory specific prey biomass during the first breeding attempt. Pairs in territories with high prey biomass restricted their range more than pairs in territories with low prey biomass. The latter sometimes even extend their activities beyond the original territory boundaries (positive values). $y = -0.11 - 0.007x$, $R^2 = 0.26$, $P < 0.002$.

clutch size (ANCOVA: $F_{6,26} = 1.50$, $P = 0.22$). Variance in the number of young fledged was significantly influenced by one factor only, the occurrence of nest predation (ANCOVA: $F_{6,26} = 10.2$, $P < 0.001$). Male and female age, time lag between female settlement and laying, territory size and prey biomass did not show significant effects on reproductive success (all $P > 0.267$).

Since the Water Pipit is a facultative double-brooded species and seven (39%) out of eighteen pairs renested after failing to fledge any young during their first breeding attempt, we also have to consider the seasonal reproductive output to get a more reliable measure of fitness. The total number of eggs laid and the total number of young fledged were again determined by the occurrence of nest-predation (Table 4). As with first breeding attempts the other factors did not explain the variance in the two measures of reproductive success.

Table 4. Summary statistics of two ANCOVA relating total number of eggs laid and total number of young fledged per season to the variables male and female age, time lag, territory size, territory-specific prey biomass and the occurrence of nest predation, respectively. Prior to analysis territory size was log-transformed.

Source of variation	SS	df	F	P
Dependent variable: Total no. of eggs laid per season				
Male age	1.304	1	0.457	0.505
Female age	6.339	1	2.224	0.148
Time lag	3.786	1	1.328	0.260
Territory size	1.669	1	0.586	0.451
Prey biomass	0.008	1	0.003	0.959
Nest predation	53.441	2	9.375	0.001
Error	71.257	25		
Model	68.379	7	3.427	0.010
Dependent variable: Total no. young fledged per season				
Male age	0.060	1	0.019	0.891
Female age	10.130	1	3.258	0.083
Time lag	0.684	1	0.220	0.643
Territory size	0.380	1	0.122	0.730
Prey biomass	5.285	1	1.700	0.204
Nest predation	39.915	2	6.418	0.006
Error	77.743	25		
Model	104.317	7	4.792	0.002

DISCUSSION

Many studies on passerines have shown a positive correlation between early breeding and reproductive success (e.g. Stutchbury & Robertson 1988, Bensch & Hasselquist 1991, Tye 1992, Lundberg & Alatalo 1992). This can arise because early birds have advantages in resource acquisition and/or are phenotypically superior. According to Brown & Orians (1970) male arrival date should be negatively related to territory size, and earlier arriving $\sigma\sigma$ should defend territories of higher quality. In reality, however, the predicted correlations between male arrival, territory size, territory quality, and hence reproductive success may be weakened under several circumstances. First, competition for better areas may be more intense,

resulting in smaller territories for early $\sigma\sigma$. Second, variation in territory size may compensate for differences in quality. Third, the predictions assume that all arriving $\sigma\sigma$ can assess the quality of a future breeding site with the same accuracy, which may not be true for birds of different age classes. Especially, birds breeding for their first year need to assess a potential territory solely on information available at the time of their arrival. Fourth, some birds may not find reliable habitat information during the period of settlement. Alpine Water Pipits, settling on the breeding grounds when the area is still covered with snow (see 'Introduction'), provide an example. So, how well can arriving birds assess future territory quality in terms of safety from predators, microclimate at the nest and food supply?

Availability of nest sites and safety from predators

Water Pipits usually use three to four different nest types which differ mainly in nest location and material (Verbeek 1970, Pätzold 1984, Böhm & Landmann 1995, Rauter 1996). Potential nest sites did not seem to be a limited resource in our study area, they were abundant in all vegetation types used as breeding habitat. Only five times (2.9%, $n = 175$) a specific nest site was re-used for breeding in the three years of study. With the exception of poorly structured meadows (vegetation units 31 and 39), that comprise only 10% of the study area, it is unlikely that a general shortage of and competition for nest sites were major factors influencing territory choice.

Secure nest sites, however, do seem to be a limited resource. Nest predation was the most important factor determining annual reproductive success in Water Pipits (Table 4). Therefore, a good territory should include a nest site with low probability of nest predation. Askenmo & Neergaard (1990) assume that in the sister species, the Rock Pipit (*Anthus petrosus*), $\text{♀}\text{♀}$ trade security against mate exclusiveness. They prefer mating in a safe place, even when this choice is associated with the cost of mate sharing. In the Water Pipit, however, the proportion of polygynous matings

translate into fitness consequences. It seems likely that in alpine habitats, and in other areas where birds do not make perfect decisions (Lenington 1980, Askenmo 1984), early arriving individuals are misled by the scarcity of available habitat information. Yet, both sexes may still benefit from early arrival; ♂♂ because of increased success in obtaining territories and mate(s); ♀♀ due to better mate choice opportunities. These benefits are especially true for older, experienced birds that have bred in the area before.

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REFERENCES

- Alatalo R.V., A. Lundberg & K. Ståhlbrandt 1984. Female mate choice in the Pied Flycatcher *Ficedula hypoleuca*. *Behav. Ecol. Sociobiol.* 14: 253-261.
- Askenmo C.E.H. 1984. Polygyny and nest site selection in the Pied Flycatcher. *Anim. Behav.* 32: 972-980.
- Askenmo C. & R. Neergaard 1990. Polygyny and nest predation in the Rock Pipit: do females trade male assistance against safety? In: J. Blondel, A. Gosler, J-D. Lebreton & R. McCleery (eds) *Population biology of passerine birds*: 331-343. Springer-Verlag, Berlin.
- Askenmo C., R. Neergaard & B. Arvidsson 1994. Food supplementation does not affect territory size in Rock Pipits. *Anim. Behav.* 47: 1235-1237.
- Bensch S. & D. Hasselquist 1991. Territory fidelity in the polygynous Great Reed Warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. *J. Anim. Ecol.* 60: 857-871.
- Biber J-P. 1982. Brutökologische Untersuchungen an einer Population des Wasserpiepers *Anthus spinoletta* (L.). Ph.D. thesis, University of Basel, Basel.
- Böhm C. 1986. Revierverhalten und Revierkriterien beim Wasserpieper (*Anthus spinoletta*). *Ökologie der Vögel* 8: 145-156.
- Böhm C. & A. Landmann 1995. Nistplatzwahl, Neststandort und Nestbau beim Wasserpieper (*Anthus spinoletta*). *J. Orn.* 1: 1-16.
- Bollmann K. 1996. The mating system of the alpine Water Pipit *Anthus spinoletta* in a variable environment: ecological, demographic and fitness aspects. Ph.D. thesis, University of Zürich, Zürich.
- Brodmann P.A. 1995. Relations between food conditions, foraging behaviour and reproductive performance in the Water Pipit (*Anthus sp. spinoletta*). Ph.D. thesis, University of Zürich, Zürich.
- Brodmann P.A., H-U. Reyser & B. Baer 1997a. The relative importance of habitat structure and of prey characteristics for the foraging success of Water Pipits (*Anthus spinoletta*). *Ethology* 103:222-235.
- Brodmann P.A., H-U. Reyser, K. Bollmann, A.R. Schläpfer & C. Rauter 1997b. The importance of food quantity and quality for reproductive performance in alpine Water Pipits (*Anthus spinoletta*). *Oecologia* 109: 200-208.
- Brooke M. de L. 1979. Differences in territory quality of territories held by Wheatears (*Oenanthe oenanthe*). *J. Anim. Ecol.* 48: 21-32.
- Brown J.L. & G. Orians 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* 1: 239-262.
- Catzefflis F. 1978. Sur la biologie de reproduction du Pipit spinocelle alpin. *Nos Oiseaux* 34: 287-302.
- Clutton-Brock T.H., F.E. Guinness & S.D. Albon 1982. *Red Deer: behavior and ecology of two sexes*. Edinburgh University Press, Edinburgh.
- Cramp S. (ed.) 1988. *The birds of the western Palearctic*, 5. Oxford University Press, Oxford.
- Cristol D.A., V. Nolan Jr. & E.D. Ketterson 1990. Effect of prior residence on dominance status of Dark-eyed Juncos *Junco hyemalis*. *Anim. Behav.* 40: 580-586.
- Davies N.B. 1991. Mating systems. In: J.R. Krebs & N.B. Davies (eds) *Behavioural ecology: an evolutionary approach*, 3rd edition: 263-299. Blackwell Scientific Publications, Oxford.
- Davies N.B. & A.I. Houston 1984. Territory economics. In: J.R. Krebs & N.B. Davies (eds) *Behavioural ecology: an evolutionary approach*: 148-169. Blackwell Science Publications, Oxford.
- Ens B.J., M. Kersten, A. Brenninkmeijer & J.B. Hulscher 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). *J. Anim. Ecol.* 61: 703-715.
- Glutz von Blotzheim U. & K.M. Bauer 1985. Hand-

- buch der Vögel Mitteleuropas, 10/II. Aula-Verlag, Wiesbaden.
- Goodburn S.F. 1991. Territory quality or bird quality? Factors determining breeding success in the Magpie *Pica pica*. *Ibis* 133: 85-90.
- Grafsoft 1992. MiniCad+ User Manual. Version 4.0. Diehl Grafsoft Inc., Elicott City, Maryland.
- Högstedt G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. *Science* 210: 1148-1150.
- Holm C.H. 1973. Breeding sex ratios, territoriality, and reproductive success in the Red-winged Blackbird (*Agelaius phoeniceus*). *Ecology* 54: 356-365.
- Lack D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- Lenington S. 1980. Female choice and polygyny in Red-winged Blackbirds. *Anim. Behav.* 28: 347-361.
- Ligon J.D. & S.H. Ligon 1988. Territory quality: key determinant of fitness in the group-living Green Woodhoopoe. In: C. Slobodchikoff (ed.) *The ecology of social behaviour*: 229-253. Academic Press, London.
- Ligon J.D. & S.H. Ligon 1989. Green Woodhoopoe. In: I. Newton (ed.) *Lifetime reproduction in birds*: 219-232. Academic Press, London.
- Lundberg A. & R.V. Alatalo 1992. *The Pied Flycatcher*. Poyser, London.
- Martin T.E. 1987. Food as a limit on breeding birds: a life-history perspective. *Ann. Rev. Ecol. Syst.* 18: 453-487.
- Parker G.A. 1974. Assessment strategy and the evolution of fighting behaviour. *J. theor. Biol.* 47: 223-243.
- Pätzold R. 1984. *Der Wasserpieper Anthus spinoletta*. Ziemsen, Wittenberg.
- Rauter C. 1996. Environmental factors, parental care and reproductive performance in the Water Pipit (*Anthus spinoletta*). Ph.D. thesis, University of Zürich, Zürich.
- SAS Institute 1994. *JMP: Statistics and Graphics Guide*, version 3. SAS Institute Inc., Cary, North Carolina.
- Seastedt T.R. & S.F. MacLean 1979. Territory size and composition in relation to resource abundance in Lapland Longspurs breeding in arctic Alaska. *Auk* 96: 131-142.
- Smith K.G. & D.C. Andersen 1985. Snowpack and variation in reproductive ecology of a montane ground-nesting passerine, *Junco hyemalis*. *Ornis Scand.* 16: 8-13.
- SPSS Inc. 1996. *SYSTAT 6.0 for Windows*. SPSS Inc. Chicago, Illinois.
- Stutchbury B.J. & R.J. Robertson 1988. Within-season and age related patterns of reproductive performance in female Tree Swallows (*Tachycineta bicolor*). *Can. J. Zool.* 66: 827-834.
- Tye A. 1992. Assessment of territory quality and its effect on breeding success in a migrant passerine, the Wheatear *Oenanthe oenanthe*. *Ibis* 134: 273-285.
- Verbeek N.A.M. 1970. Breeding ecology of the Water Pipit. *Auk* 87: 425-451.
- Verbeek N.A.M. 1981. Nesting success and orientation of Water Pipit *Anthus spinoletta* nests. *Ornis Scand.* 12: 37-39.
- Verner J. & M.F. Willson 1966. The influence on habitats on mating systems of North American passerine birds. *Ecology* 47: 143-147.
- Von Haartman L. 1990. Breeding time of the Pied Flycatcher *Ficedula hypoleuca*. In: J. Blondel, A. Gosler, J-D. Lebreton & R. McCleery (eds) *Population biology of passerine birds*: 1-16. Springer-Verlag, Berlin.
- Weatherhead P.J. & R.J. Robertson 1977. Harem size, territory quality, and reproductive success in the Redwinged Blackbird (*Agelaius phoeniceus*). *Can. J. Zool.* 55: 1261-1267.
- Wittenberger J.F. 1976. The ecological factors selecting for polygyny in altricial birds. *Am. Nat.* 110: 779-799.
- Zumbühl G. & J. Burnand 1986. Vegetationskarte Davos-Parsenn-Dischma. 1 : 25.000. In: O. Wildi & K. Ewald (eds) *Der Naturraum und dessen Nutzung im alpinen Tourismusgebiet von Davos: Ergebnisse des MAB-Projektes Davos*. Beilage. Eidg. Anstalt für forstliches Versuchswesen, Birmensdorf.

SAMENVATTING

Het broedsucces van vogels kan afhankelijk zijn van verschillen tussen territoria wat betreft voedselrijkdom, veiligheid voor nestpredatoren en microklimatologische omstandigheden bij het nest. Echter, in veel biotopen zijn deze kwaliteitskenmerken van de broedterritoria, en daarmee het verwachte broedsucces, moeilijk te schatten op het moment dat een territorium wordt gevestigd. In deze studie wordt een poging ondernomen om de kwaliteit te meten van de broedterritoria van Waterpiepers in de Zwitserse Alpen, en deze te relateren aan vestigingspatronen en broedsucces. Binnen het studiegebied bestonden grote verschillen in rijkdom aan voedsel (voornamelijk insecten) tussen de verschillende vegetatietypen waar Waterpiepers gebruik van maakten. Er was een toename in voedselrijkdom in de loop van het broedseizoen en voedselrijkdom per terri-

torium was negatief gecorreleerd met de mate van sneeuwbedekking bij het begin van het broedseizoen. De meeste ♂♂ kwamen voor de ♀♀ in het studiegebied aan, en beide seksen vestigden zich in voedselrijke gebieden eerder dan op relatief voedselarme plaatsen. Vroege ♂♂ bezetten ook grotere territoria, en vroeg arriverende ♀♀ deden er langer over om vanaf vestiging met de eileg te beginnen dan latere ♀♀. Maar broedselgrootte en het aantal jongen dat per broedpoging en per seizoen werd geproduceerd waren niet gecorreleerd met voedselrijkdom, territoriumgrootte, tijd tussen aankomst en eileg en de leeftijd van ♂♂ of ♀♀. Het enige dat verband hield met broedsucces was de

mate van nestpredatie, maar deze factor was op geen enkele manier gecorreleerd met de omgevingsvariabelen. De vogels zelf konden de kwaliteit van het territorium of broedsucces kennelijk ook niet voorspellen want het vestigingspatroon van beide seksen had niets te maken met de latere nestpredatie. De auteurs bespreken de redenen waarom Waterpiepers territoriumkwaliteit niet kunnen meten op het moment dat ze hun keuze moeten maken, en wat voor alternatieven ze hebben om zich op dat moment toch ergens te vestigen. (TP)

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Appendix A. Classification and characterization of the vegetation in the study area. Eight vegetation units (after Zumbühl & Burnand 1986) were grouped into five vegetation types according to the abundance of various dwarf shrubs and the management practise. Characteristics of the five vegetation type (1) Most intensively managed vegetation, restricted to the valley bottom and lower slopes, partially used for hay production (31; no bushes, not used as breeding habitat) or as pastures (22, 29, 43; some bushes, regularly used as breeding habitat). (2) Typical and widely distributed vegetation of the valley slopes, frequently used as breeding habitat. (3) Rare dwarf shrub vegetation, restricted to the valley bottom, frequently used as breeding habitat. (4) Most widespread vegetation of the valley slope, frequently used as breeding habitat. (5) Rare vegetation type and the only one with plants more than 1 m in height, ground vegetation comparable to type 4, in addition loose *Alnus* or *Betula* bushes, only exceptionally used as breeding habitat.

Vegetation units	Vegetation type	%
22 <i>Caricetum fuscae</i>	1 Subalpine meadows and pastures	27
31 <i>Polygono-Trisetion</i>		
39 <i>Poion alpinae</i>		
43 <i>Nardion</i>		
20 <i>Junipero-Arctostaphyletum callunetosum</i>	2 Medium sized dwarf shrub dominated by <i>Calluna</i>	18
16 <i>Rhododendro-Vaccinetum</i>	3 Large sized dwarf shrub dominated by <i>Rhododendron</i>	6
19 <i>Junipero-Arctostaphyletum</i>	4 Large sized dwarf shrub dominated by <i>Juniperus</i> and <i>Vaccinium</i>	44
14 <i>Alnetum viridis</i>	5 Large sized dwarf shrub dominated by <i>Alnus</i> and <i>Betula</i>	6