Ardea **85**: 83-98

Territory quality and reproductive success: can Water Pipits *Anthus spinoletta* assess the relationship reliably?

BOLLMANN, K., REYER, H.-U. & BRODMANN, P.A.

Zoologisches Institut, Universität Zürich,
Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

corresponding author: H.-U. Reyer
phone: +41-1-257 49 89
Fax : +41-1-363 31 85
e-mail: ulireyer@zool.unizh.ch

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ABSTRACT

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 also negatively correlated to snow cover during the pre-breeding period. Males, on average, arrived prior to females, and both sexes settled earlier in prey-rich than in prey-poor areas. Early settling males also occupied larger territories, early settling females 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.

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 males, 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 existence 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 limiting 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 male 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 males 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 males 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 rational 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 & Bauer (1985) and Cramp (1988). Territory establishment is exclusively done by the males. 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, males 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).

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 1990–93 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 km^2 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° ($x \pm SD = 23 \pm 12.0°$). Details about the weather and climate of the study area are found in Bollmann (1996). The vegetation of the valley had 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:

(I) subalpine meadows and pastures (22, 31, 39, 43);
(II) medium sized dwarf shrub dominated by *Calluna* (20);
(III) large sized dwarf shrub dominated by *Rhododendron* (16);
(IV) large sized dwarf shrub dominated by *Juniperus* and *Vaccinum* (19);
(V) large sized dwarf shrub dominated by *Alnus* and *Betula* (14).

These five vegetation types increase in height and prey biomass. Type V differs from type IV only by the presence of scattered *Alnus* and *Betula* bushes, the ground vegetation is equal. Since no prey sampling was practicable in vegetation type V, its prey biomass was equated with that of type IV. 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 V 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 50x50m 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 standardised 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 female 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 biomass 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 to 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 males and 41% of the females 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).

Settlement and territoriality: 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 male was observed on the ground where he subsequently showed territorial behaviour or to the first day a female 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 individuals every third or fourth day. Daily observation were conducted from dawn to 1 p.m. and from 5 p.m. 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 males and females, 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 males. These included starting and landing points of song-flights, perches of lookout posts, sites of male-male 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 males 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 male 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).

Nest search and nest monitoring: 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 females, by watching females 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 lest 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 backdating.

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).

Measures of reproductive success: 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

(1) 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 the first territory establishment in this year.

A multiple regression analysis (path 1 in Fig. 1) relating snow (C) cover 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) 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 II, IV and V, had less snow than flat areas at low altitudes, including those near the valley bottom, where vegetation types I and III are concentrated (Fig. 3a). This relationship diminished within the process of snow melting (Fig. 3b).

(2) Ecological correlates of prey biomass and predation

(a) Prey biomass: 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 (II, III, IV) had consistently higher prey biomass than areas with meadows and pastures (I), 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 (I) and prey-rich (II, III, IV).

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 2-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.

(b) Predation: 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 first 10 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 occurence 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: χ^2_7=13.40, *p*=0.063, *n*=39), suggesting that the set of variables considered does not allow males 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 (χ^2_2=10.23, *p*=0.037, *n*=39). Predation rates at nests of one, two and three year old males were 72.7, 54.6 and 0.0%, respectively (*n*=22, 11, and 6).

(3) 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 3 days later (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 I) and prey-rich shrub vegetation (types II-IV; cf. p.13 and Appendix A) it is obvious that the latter is settled earlier (p=0.016).

(4) 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, males and females (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 females initiated clutches about one to two weeks after pair formation, whereas early females 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 days. Male settlement was further related to territory size. Early settling males defended bigger territories. During the FBP seven (15%) out of 46 males 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 males. Although the difference was not significant (Wilcoxon 2-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: χ^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 (Chi-square test: χ^2_1=7.53, p<0.01, n=34).

(5) 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 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.

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 males 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 males. Second, variation in territory size may compensate for differences in quality. Third, the predictions assume that all arriving males 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*), females 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 did not differ between valley sides with frequent and rare nest predation (Schläpfer, unpubl. data). According to Wittenberger (1976) the information available for direct habitat selection increases as the season progresses, and Bensch & Hasselquist (1991) mention that the costs of loosing time through late arrival can be overcome by the benefits of occupying a high quality territory. Since nest predation appeared to be largely stochastic in the Water Pipit population under study, and was not significantly related to recognizable environmental conditions, predation risk probably cannot be estimated reliably at any time (at least not by first time breeders), and delayed settlement is unlikely to improve assessment of territory quality in terms of safety.

Microclimate and snow at nest sites:

Female Water Pipits show a preference for nest sites that guarantee some protection from the prevailing wind, possible snow drifts and direct sun light (Verbeek 1981, Biber 1982, Böhm & Landmann 1995, Rauter 1996). During the period between settlement and the start of breeding (on average 18 days), females were observed to inspect various nest sites and they sometimes remained for minutes at such a site. In this way, they probably examined microclimatic conditions. The occasional re-use of a nest site by a different female may also indicate specific nest-climate or site preferences (Böhm & Landmann 1995). Nest site selection is a time consuming activity that is done after settlement. During settlement, most future nest sites lay below snow and could not be evaluated during territory choice (Biber 1982, Böhm & Landmann 1995, own observations).

Although microclimatically advantageous sites may be found in most of the territories and did not seem to be limiting in benign weather, reproductive success can depend on site quality under extreme climatic conditions. In 1991, a mid-June snow led to the desertion of 32% of 41 active nests. Vulnerability of nests to snow varied with the structural characteristic of the vegetation immediately covering them: nest failure was highest in vegetation type II (66.7%), followed by types I (27.8%), IV (18.2%) and III and IV (0.0% each). The interesting point is that experienced females, in contrast to one year old females, chose territories where the risky vegetation type II was significantly underrepresented (unpubl. data). Since spring and June snow falls are common in the study area and the 1991 snow level was typical for the 10-year average (Bollmann 1996), snow may cause strong selection against early breeding. However, snow cover did not determine the settlement pattern directly, a result that agrees with Biber (1982). In other studies of territorial passerines breeding in arctic or alpine habitats, Seastedt & MacLean (1979), Catzeflis (1978) and Böhm (1986) found early settlement of males in areas where snow melting was progressed; but these authors did not consider further confounding environmental factors in their analyses.

The importance of food supply

Early arriving males and females preferably settled in dwarf shrub areas where prey biomass during first and later breeding attempts was higher than in grass areas. Territory-specific food supply, however, did not affect reproductive success, probably because later in the season food apparently was plentiful. This is suggested by our finding that most birds reduced their home ranges when incubating eggs and feeding young (Fig. 6). Also, using data from three years and two study sites each, we did not find any density-dependent variation in reproductive success (Bollmann 1996, Schläpfer, unpubl. data). Thus, territory-specific food supply is unlikely to be a limiting resource once Water Pipits feed their nestlings; but it may be early in the season. Early birds may be forced to settle in relatively prey-rich areas in order to satisfy their own energetic needs which include costs of territorial defence in males and egg production in females. According to this explanation, the early settlement in prey-rich vegetation partly results from opportunistic habitat choice during a time of severe food conditions and small population density. Although the actual energy budget is modified by vegetation-specific searching and handling times as well as by prey-specific energy content, the prey density investigated in this study remains the best predictor of profitability (Brodmann *et al.* 1997a,b).

Other advantages of early settlement

Even where settlement patterns are not related to any territory quality measure potentially affecting reproductive success, birds may benefit from early arrival for other reasons. Males can establish a large and prey-rich territory (Table 3) which not only may be beneficial in satisfying their own energy demands (see above); it also seems to help in attracting a female (or multiple females), as indicated by the apparently positive relationship between territory size and the probability of becoming paired (p=0.076; see also Bollmann 1996). The later males arrive, the more they suffer from direct competition with other males and the very late ones may fail completely to settle in a territory and to mate. For the Rock Pipit, Askenmo *et al.* (1994) give some evidence that territory owners have a competitive advantage even when disfavoured by an asymmetry in their phenotypic resource-holding potential (RHP), a term coined by Parker (1974) for the constellation of factors that influence an animal’s fightinh ability. If the RHP of older Water Pipits is usually higher than that of new breeders, but the latter can increase their success by settling early, then intrasexual competition may have led to directional selection for earlier male arrival. This may be one reason why we did not find an age biased return schedule common to other species (e.g. Brooke 1979, Alatalo *et al.* 1984). Another, not mutually exclusive, explanation is that birds arriving from migration do not immediately establish their territories permanently. Rather, they move back and forth between the breeding sites and the lower valley areas for several days or even weeks, depending on weather conditions (see Introduction).

While males may forego the chance of obtaining a large and good territory and/or one or two mates when settling late, there was no detectable reproductive disadvantage for late settling females. This can be explained by the negative correlation between settling and breeding dates (Table 3), which synchronizes egg laying in spite of large variation in settlement. The time lag between settlement and clutch initiation was not related to territory-specific food supply (Bollmann 1996). The longer time lag of early arriving females may reflect both the need to avoid highly probable nest failure due to spring snow falls and difficulties in forming eggs so early in the season. The figure of six days for the minimum time lag coincides well with the final rapid growth of oocytes (5 days) in the Pied Flycatcher *Ficedula hypoleuca* (von Haartman 1990). Females may differ in where and how they obtain the necessary energy, with some settling early in prey-rich areas of the breeding habitat and others arriving later after prolonged foraging further down the valley.

For both sexes, the decision when to settle may also be affected by age, which - at least in females - was tendentially related to the total number of young fledged (Table 4). Older birds, that have bred in the same area before, are less dependent on immediate habitat information than first year breeders, because experienced birds can base their territory choice on previous information about the risk that nests will be predated or covered by snow. In Water Pipits, this is illustrated by the observed decrease in nest predation rates with increasing age of the male owner and by the fact that older females avoided to nest in vegetation type II which is most susceptible to snow. Thus, older birds seem to have a competitive advantage at the time of arrival when territory quality cannot be assessed directly. With a scarcity of direct habitat information during the period of settlement and pairing we expect females to base their decision "Where to settle and to mate?" on mate characteristics (i.e. age) rather than on habitat features. Early females may benefit from a larger pool of unmated males for mate choice.

In conclusion, nest predation - the major factor determining reproductive success - was unrelated to settlement patterns of males and females, suggesting that it cannot be assessed reliably upon arrival. In contrast, direct and/or indirect measures of prey biomass were used by both sexes as indicators of territory quality, but these factors did not 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; males because of increased success in obtaining territories and mate(s); females due to better mate choice opportunities. These benefits are especially true for older, experienced birds that have bred in the area before.

ACKNOWLEDGEMENTS

We are grateful to numerous people who carried out additional studies in the Water Pipit Group of the University of Zürich and contributed important information: Fredy Frey-Roos, Hannes Geisser, Claudia Rauter and Alex Schläpfer. Nils Tonascia helped to modify the CAD-software for territory analysis. We thank Tim H. Clutton-Brock for valuable discussions, and Martin Weggler, Dik Heg and one anonymous reviewer who provided useful comments on an earlier version of this manuscript. Research reported in this paper was financed by the Swiss National Foundation (SNF) through a grant to Prof. H.-U. Reyer (No. 31–26308.89).

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FIGURE LEGENDS

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 bold numbers correspond to the statistical analyses and headings in the Results-section.

Fig. 2. Vegetation map of the study site after Zumbühl & Burnand (1985): 14=*Alnetum viridis*, 16=*Rhododendro-Vaccinetum*, 19=*Junipero-Arctostaphyletum*, 20=*Junipero-Arctostaphyletum callunetosum*, 22=*Caricetum fuscae*, 31=*Polygono-Trisetion,* 39=*Poion alpinae*, 43=*Nardion*. The study area (within the thick line) was divided into two connected plots A and D.

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 50x50m 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 botton. This relationship gets lost within the process of snow melting (b).

Fig. 4. Phenology of snow melting (dots) and prey biomass (open circles; mg dryweight / 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 by arrows. M = median date of settlement.

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).

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). $y=-0.11-0.007x$, $r^2=0.26$, $p<0.002$.

Table 1. Comparison of prey biomass (mg drymass / 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: I=meadows and pastures, II=medium sized dwarf shrub dominated by *Calluna*, III=large sized dwarf shrub dominated by *Rhododendron*, IV=large sized dwarf shrub dominated by *Juniperus* and *Vaccinum*. Data given are means±1SE, sample sizes in parenthesis. Significance levels: *$p<0.05$, **$p<0.01$, ***$p<0.001$.

Vegetation type	Breeding period		
	First	Late	Overall
I	1.24±1.73 (62)	4.09±11.49 (10)	1.57±2.59 (75)
II	10.31±3.52 (15)	33.49±14.83 (6)	14.18±4.39 (26)
III	7.94±4.55 (9)	55.08±25.59 (2)	18.42±6.47 (12)
IV	20.74±1.93 (50)	56.07± 9.08 (16)	26.38±2.50 (80)
[1]*H*=	73.793***	15.807**	79.617***

[1] Kruskal-Wallis 1-way ANOVA:

First breeding period, U-tests: I vs. II, **; I vs. III, ***; I vs. IV, ***; II vs. III, **; II vs. IV, ns; III vs. IV, ns (p=0.06).

Late breeding period, U-tests: I vs. II, *; I vs. III, ***; I vs. IV, *; II vs. III, ns; II vs. IV, ns; III vs. IV, ns.

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 of variation	Sum of squares	*df*	*F*-value	*p*-value
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

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 prohabilities are two-tailed: *p<0.05, **p<0.01, ***p<0.001, others p>0.05.

Variables:	Male settlement		Female settlement	
	n=	r_S=	*n*=	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

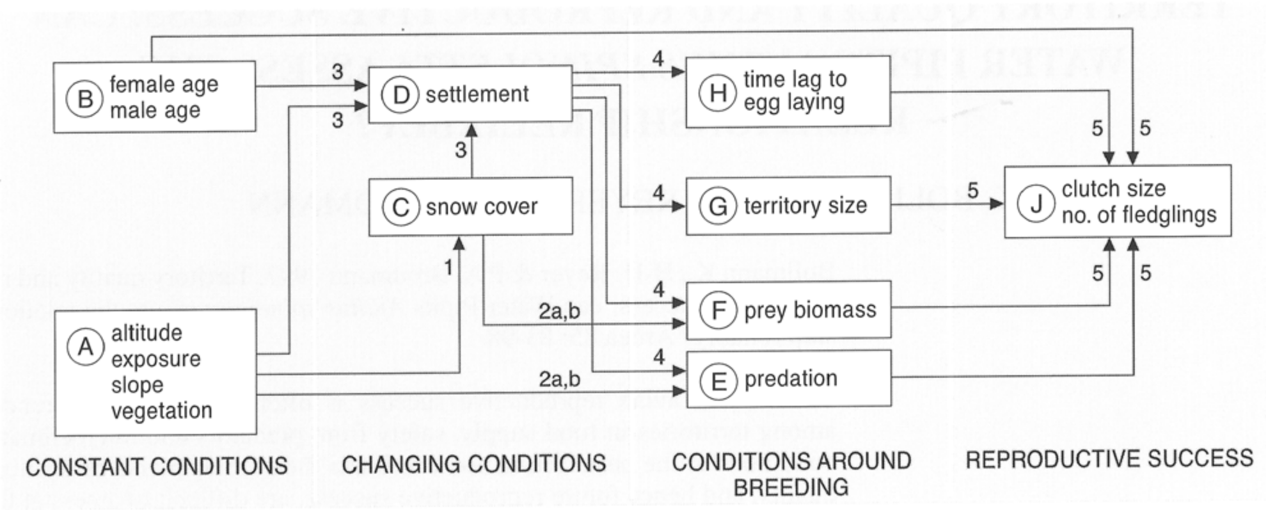
Table 4. Summary statistics of two ANCOVA relating total number of eggs laid and total number of young fledged per season to the variables male and female age, time lag, territory size, territory-specific prey biomass and the occurrence of nest predation, respectively. Prior to analysis territory size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

Dependent variable:	Total no. of eggs laid per season			
Source of variation	Sum of squares	*df*	*F*=	*p*=
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			
Source of variation	Sum of squares	*df*	*F*=	*p*=
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

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.

Vegetation units		Vegetation type		Proportion (%)	Characteristics
22 31 39 43	*Caricetum fuscae* *Polygono-Trisetion* *Poion alpinae* *Nardion*	I	Subalpine meadows and pastures	27	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).
20	*Junipero-Arctostaphyletum callunetosum*	II	Medium sized dwarf shrub dominated by *Calluna*	18	Typical and widely distributed vegetation of the valley slopes, frequently used as breeding habitat.
16	*Rhododendro-Vaccinetum*	III	Large sized dwarf shrub dominated by *Rhododendron*	6	Rare dwarf shrub vegetation, restricted to the valley bottom, frequently used as breeding habitat.
19	*Junipero-Arctostaphyletum*	IV	Large sized dwarf shrub dominated by *Juniperus* and *Vaccinum*	44	Most widespread vegetation of the valley slope, frequently used as breeding habitat.
14	*Alnetum viridis*	V	Large sized dwarf shrub dominated by *Juniperus*, *Vaccinum* and *Alnus*	6	Rare vegetation type and the only one with plants more than one meter in height, ground vegetation comparable to type IV, in addition loose *Alnus* or *Betula* bushes, only exceptionally used as breeding habitat.

Figure 1



B female age male age
D settlement
H time lag to egg laying
C snow cover
G territory size
J clutch size no. of fledglings
A altitude exposure slope vegetation
F prey biomass
E predation
1
2a,b
2a,b
3
3
3
4
4
4
4
5
5
5
5
5
CONSTANT CONDITIONS
CHANGING CONDITIONS
CONDITIONS AROUND BREEDING
REPRODUCTIVE SUCCESS

Figure 2

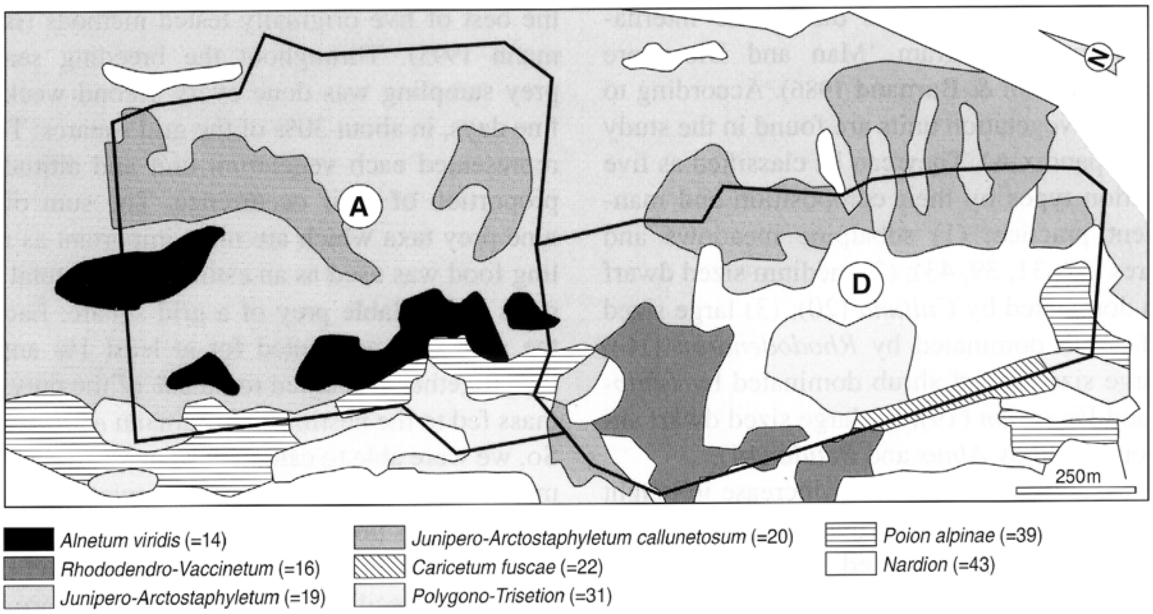

N
A
D
250m
Alnetum viridis (=14)
Rhododendro-Vaccinetum (=16)
Junipero-Arctostaphyletum (=19)
Junipero-Arctostaphyletum callunetosum (=20)
Caricetum fuscae (=22)
Polygono-Trisetion (=31)
Poion alpinae (=39)
Nardion (=43)

Figure 3

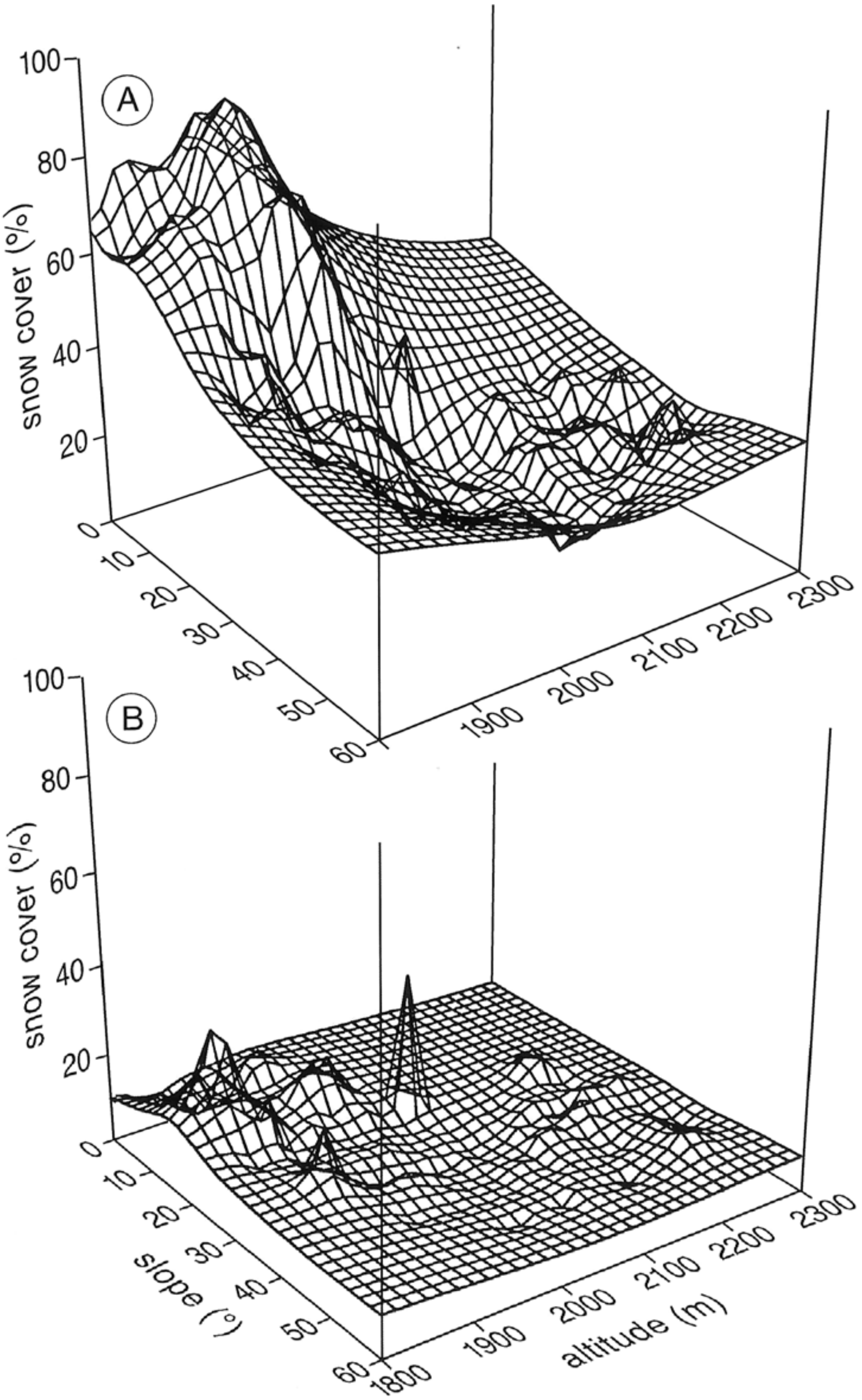

A
B
snow cover (%)
0
20
40
60
80
100
slope (°)
0
10
20
30
40
50
60
altitude (m)
1800
1900
2000
2100
2200
2300

Figure 4

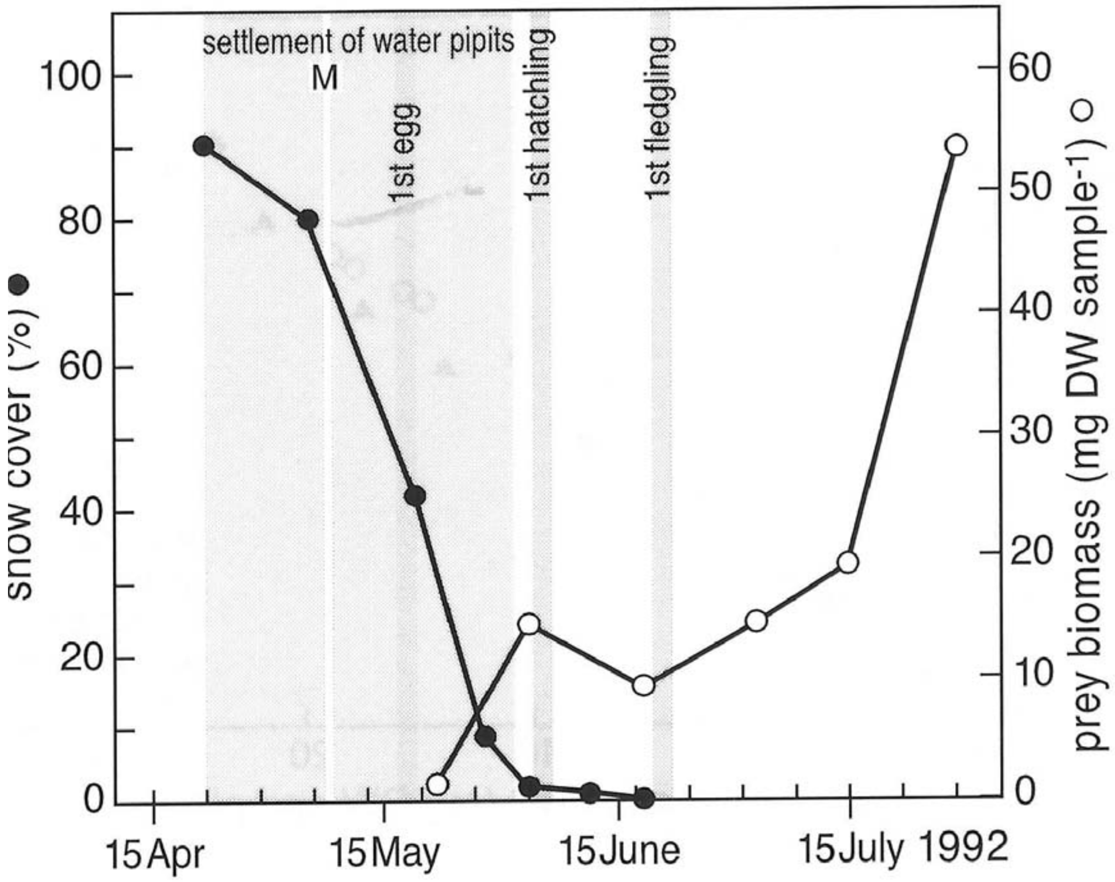

settlement of water pipits
M
1st egg
1st hatchling
1st fledgling
snow cover (%) ●
prey biomass (mg DW sample^{-1}) ○
0
20
40
60
80
100
0
10
20
30
40
50
60
15 Apr
15 May
15 June
15 July 1992

Figure 5

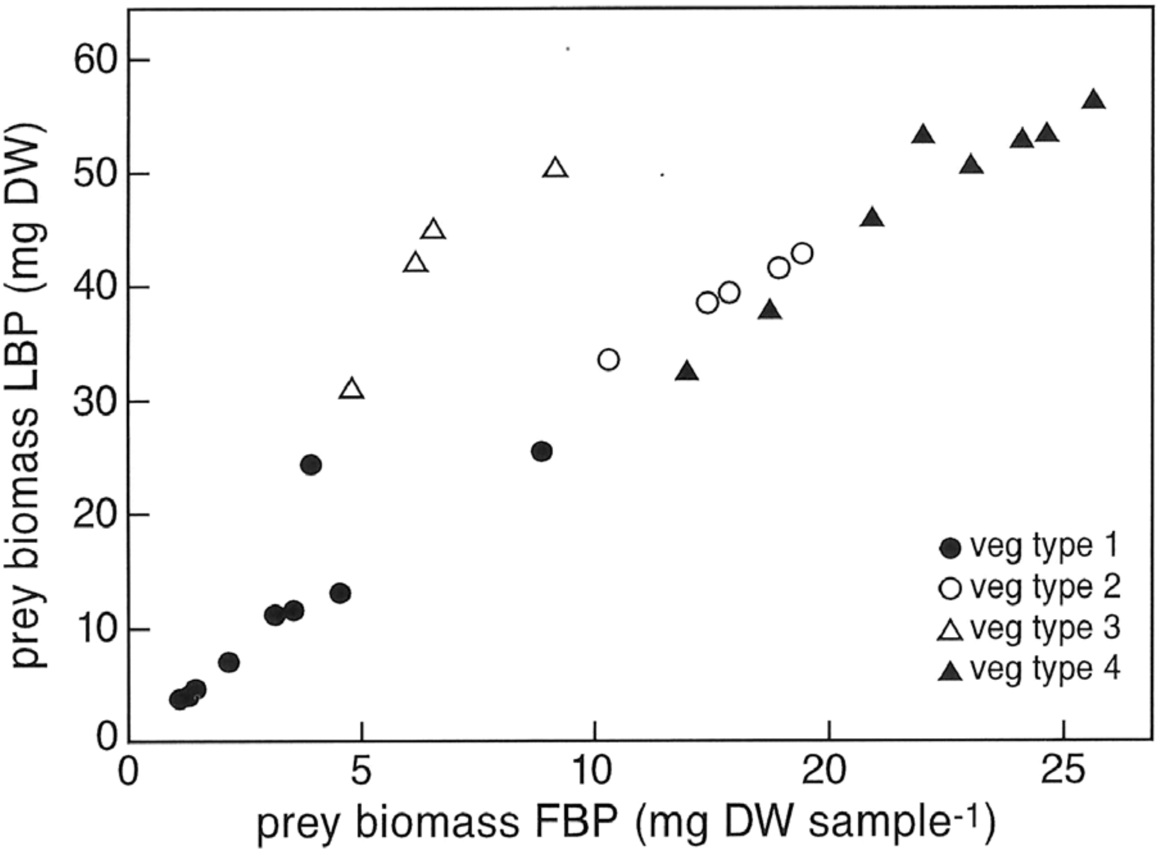

prey biomass LBP (mg DW)
60
50
40
30
20
10
0
0
5
10
20
25
prey biomass FBP (mg DW sample-1)
● veg type 1
○ veg type 2
△ veg type 3
▲ veg type 4

Figure 6