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Authors: van Dijk, René E., Pilon, Arjen E., Szentirmai, István, Székely, Tamás, and Komdeur, Jan

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The influence of habitat structure on sexual conflict over care in Penduline Tits *Remiz pendulinus*

René E. van Dijk[1,2,*], Arjen E. Pilon[2], István Szentirmai[3], Tamás Székely[1] & Jan Komdeur[2]

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Spatial and temporal distributions of resources and habitats often influence breeding systems. These influences are particularly relevant in those species that exhibit variable breeding systems. We studied such a species, the Penduline Tit *Remiz pendulinus*. This small passerine bird has sequential polygamy by both sexes, and evidence suggests intense sexual conflict between males and females over care. We estimated habitat structure by scoring the vegetation important for nest building and foraging in the immediate surroundings of the nest. Using four principal components we show that sites with more abundant vegetation are occupied earlier than sites with sparse vegetation. However, habitat structure does not predict mating success or reproductive success, and it neither predicts which parent (the male, the female or both) deserts the clutch. We therefore suggest that habitat structure does not have a direct effect on reproductive success or on the resolution of sexual conflict in Penduline Tits. Specific aspects of habitats, such as food and nest material availability, remain to be tested.

Key words: habitat structure, sexual conflict, Penduline Tit, reproductive success, mating success

[1]Department of Biology and Biochemistry, University of Bath, Claverton Down, Bath BA2 7AY, UK; [2]Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Biological Centre, P.O. Box 14, 9750 AA Haren, The Netherlands; [3]Őrsèg National Park, Siskaszer 26a, H-9941, Őriszentpéter, Hungary;
*corresponding author (R.E.van.Dijk@bath.ac.uk)

INTRODUCTION

The distribution and availability of resources often influence breeding systems in birds. The degree of spatial homogeneity of distribution of resources, for instance, influences the way males establish territories and subsequently the number of females they may obtain (Verner 1964, Verner & Wilson 1966, Orians 1969, Bennett & Owens 2002). Abundant food often promotes polygamy (Davies 1991, Andersson 2005). However, the link between food availability and breeding system is likely to be more complicated than often anticipated (Kosztolányi *et al.* 2006). For instance, interference competition, the competitive interaction between individuals over resources, appears to play an important role in the distribution of individuals (Kosztolányi *et al.* 2006, Vahl 2006). These distributions in turn, may affect mate availability and thus the costs and benefits of desertion (Emlen & Oring 1977, Alatalo *et al.* 1981, Davies 1989, Székely *et al.* 1999).

One of the drivers of breeding system evolution is sexual conflict; this emerges if the evolutionary interests of males and females over reproduction are different (Davies 1992, Birkhead & Parker 1997, Houston *et al.* 2005, Thomas *et al.* in press). In species where there is sexual conflict over care provisioning, such as the Dunnock *Prunella modularis* (Davies 1992), Kentish Plover *Charadrius alexandrinus* (Székely *et al.* 1999), or the Snail Kite *Rostrhamus sociabilis* (Beissinger 1987), food abundance may play an important role in resolving this conflict. In polygamous species, for instance, high food availability may allow females to lay subsequent clutches, with males having to care for the young (Andersson 2005). Furthermore, high food availability may promote the existence of sexual conflict as it promotes the sufficiency of uniparental care for the survival of offspring, opening up the possibility for one parent, either male or female, to desert. In the Snail Kite, for instance, mate desertion occurs more frequently when food is abundant (Beissinger 1987). Which parent deserts may depend on ecological factors in species with plastic expression of alternative breeding strategies (Emlen & Oring 1977, Davies *et al.* 1995, Székely *et al.* 1999, Wysocki 2004, Magellan & Magurran 2006). For instance, if there are many unpaired males available in a population, the female may more likely desert than the male, if either parent can care for the offspring on its own. Similarly, if the remating opportunities are better for males, males are more likely to desert.

Here we investigate whether habitat structure, as a proxy measure for food and nest material availability, influences the outcome of sexual conflict over parental care in Penduline Tits *Remiz pendulinus*. Sexual conflict in this small passerine is exhibited by parental care always being carried out by one parent, either by the male (5–20%), or by the female (50–70%). In addition, some 30–40% of clutches is deserted by both parents during egg-laying (Persson & Öhrström 1989). This pattern of parental care suggests intense sexual conflict over care. Szentirmai *et al.* (2007) recently showed that both males and females gained by deserting, but both pay a cost if their mate does so. Furthermore, the process of desertion is rapid: biparental desertion takes place within one or at most within two days, suggesting an arms race for deserting first (van Dijk *et al.* 2007).

Parental care is costly in terms of survival, energy and remating opportunities (Dijkstra *et al.* 1990, Webster 1991, Székely *et al.* 1996, Magrath & Komdeur 2003). Therefore, each parent is expected to shift care to its mate (Houston *et al.* 2005). One may expect that habitat structure influences the observed pattern of care. Given that clutches cared for by females are significantly larger (5.8 ± 1.3 eggs) and are thus likely to have a higher energy demand than clutches cared for by males (3.5 ± 1.4 eggs, van Dijk *et al.* 2007), female-only care is expected to be more prevalent in food rich habitats, whereas male-only care may be more frequent in habitats with low food availability. Food rich habitats will be beneficial for both male and female: the female is more likely to successfully raise the young. This would offer the male the opportunity to desert. However, if there is little food available, the female might try to preempt desertion by the male, attempting to force him to care (Lazarus 1990, Barta 2002). We would therefore predict that males would occupy food-rich habitats first after returning from their wintering grounds. A similar argument can be made in regards to nest material availability: female-only care is expected in habitats offering more nest material. Females are likely to care for males that spend more time on nest building and also for males that build large nests (Szentirmai *et al.* 2005). This offers the males the opportunity to desert and avoid the costs of parental care. In sum, males are expected to occupy habitats that have dense vegetation and abundant nest material first.

METHODS

Study species

The Penduline Tit is a small passerine (body mass about 9–10 g), and has a widespread distribution across Europe and Asia. It exhibits sequential polygamy by both sexes, and both male and female may have up to six partners in a single breeding season (Persson & Öhrström 1989, Houston *et al.* 2005, Szentirmai *et al.* 2007).

We studied Penduline Tits in Hungary (see below). Penduline Tits were ringed with a unique combination of three colour-rings and one numbered metal ring (Bleeker *et al.* 2005). Standard morphometric measurements were taken. The size of the eye-stripe (the 'mask') of the birds, signalling attractiveness, was measured using digital photographs and analysed using Adobe Photoshop 7.0 (Kingma *et al.,* unpubl. data). In total there were 177 and 158 nests in 2004 and 2005, respectively. Of the 62 males and 44 females we colour-ringed in 2004, only three males and one female were re-sighted in 2005. We searched the complete study area for new, unpaired, nest-building males, and visited each active nest (i.e. in nest-building, egg-laying, incubating, or feeding phase) nearly every other day (van Dijk *et al.* 2007). At each nest the following dates were recorded: (i) Nest initiation date. The exact date could be determined for nests found at the date of initiation of nest building, when only a small amount of material is woven around a twig (Cramp *et al.* 1993). For nests in later stages of development, the nest initiation date could be estimated using nests found on the day of nest-building initiation as a reference (Szentirmai *et al.* 2005). (ii) Date of pair formation. A male was considered to be mated as soon as the pair was seen copulating near the nest, or building the nest together. (iii) Date of desertion. A nest was considered to be deserted by one or both of the parents if a male or female (or both) was not seen at the nest for at least 15 minutes for at least two consecutive nest checks. A 15-minute period appears to be enough to establish the presence of a bird at its nest (van Dijk *et al.* 2007). Mating time was defined as the number of days it took a male to attract a mate from the date it started building its nest. Mating success was defined as whether pair formation took place or not. Dates are given as number of days since 1 March in each year.

Habitat structure

Data were collected in 2004 and 2005 in Fehértó (1321 ha) in southern Hungary (46°19'N, 20°5'E). From 7 May to 15 June in 2004, and from 18 May to 10 July in 2005 habitat structure was investigated for 48 and 139 nests, respectively. Fehértó is an extensively used fish farm consisting of large fishponds separated by dikes. The Reed beds *Phragmites australis* were along the dikes, and Penduline Tits built their nests in Willows *Salix* spp., Poplars *Populus* spp. and Russian Olives *Eleagnus angustifolius* – the reeds and these trees were used both for foraging and searching for nest material (Cramp *et al.* 1993, Darolová & Krištofík 1993, Glutz von Blotzheim 1993, Krištín 1995, Grubbauer & Hoi 1996, Szentirmai 2005). Penduline Tits in our study area mainly foraged on Poplars, Willows and Reed, as also reported by Krištín (1995) and Cramp *et al.* (1993), but rarely on Russian Olives (A. wa Kang'eri & D.M. Brinkhuizen, unpubl. data). In addition, nestling feeding rates seemed to increase with habitat structure, estimated as the number of trees and coverage of reed within 50 m surrounding the nest (see below; A. wa Kang'eri & D.M. Brinkhuizen, unpubl. data). The above trees and reed made up the vast majority of vegetation in our study area. Elder *Sambucus nigra* and Black Locust *Robinia pseudoacacia* also occurred, but they were rarely used for nest building (R.E. van Dijk unpubl. data, Darolová & Krištofik 1993). The remaining vegetation in the area may consist of grass or agricultural lands; both are unsuitable for foraging or collection of nest material by Penduline Tits. There was, however, variation in the constitution of the above vegetation surrounding the different nests in our study site, varying from only a few trees with no more than five percent reed cover to small patches of wood surrounded by wide reed beds.

Habitat structure was scored within a radius of 50 m around each nest. The minimum distance between simultaneously active nests is approximately 50 m (Glutz von Blotzheim 1993). Within this radius we counted the number of live Poplars, Willows and Russian Olives. A distinction between large and small trees was made as follows: for Poplars, 'small Poplar': trunk circumference at 1.5 m height <60 cm; 'large Poplar' trunk circumference at 1.5 m ≥ 60 cm; Poplars shorter than 1.5 m were not counted. For Willows we estimated the percentage of daylight covered by leaves, i.e. canopy density, in combination with the height of the tree, which was used as follows: 'small Willow': canopy density <50%, irrespective of tree height, or canopy density ≥ 50% and tree height ≤ 6 m; 'large Willow' tree height >6 m. Two observers carried out tree counts in 2004. In 2005 trees were counted by a third observer. Reed coverage in the above area was estimated by drawing a sketch of the vegetation from which coverage was estimated visually to 5% accuracy. All reed estimates were carried out by one observer in both years.

Data analyses

Variables describing the habitat structure were multi-collinear, we therefore carried out a principal component analysis (PCA) to extract four principal components (PCs) using varimax rotation with Kaiser normalisation. These four components together explained 81.2% of the variance in habitat structure (Table 1), and they did not differ between the two years of study (Mann-Whitney *U*; $P > 0.104$, $n = 187$). PC1 mainly accounts for the number of Poplars, PC2 for the number of Russian Olives, PC3 for the number of Willows, and PC4 mainly accounts for reed coverage (Table 1).

Table 1. Factor loadings of each variable, eigenvalue per component and percentage of variance explained by each component of the principal component analysis. Significance of correlation: * $P < 0.05$, ** $P < 0.001$. Absolute values of factor loadings >0.7 are in bold.

	PC1	PC2	PC3	PC4
Reed coverage	0.085	–0.002	–0.091	**0.977****
Large Willows	0.099	–0.148*	**0.781****	–0.125
Small Willows	0.002	0.045	**0.863****	0.014
Large Poplars	**0.916****	–0.010	–0.032	0.010
Small Poplars	**0.882****	0.059	0.142	0.097
Large Russian Olives	0.083	**0.875****	–0.081	0.192*
Small Russian Olives	–0.032	**0.897****	–0.023	–0.186*
Eigenvalue	1.643	1.597	1.392	1.052
% variance accounted for	23.5	22.8	19.9	15.0

Table 2. Descriptive statistics of response variables.

	Mean ± SD	Range	*n*
Date of nest-building initiation	92.7 ± 21.3	34–132	56
Male mask size (cm^2)	1.36 ± 0.25	0.80–1.79	41
Mating time (days)	8.3 ± 7.2	0–35	46
Number of eggs	4.2 ± 1.9	1–8	46
Number of chicks	3.7 ± 1.6	1–7	29
Hatching success (%)	68.9 ± 21.2	33.3–100.0	33

We used these PCs as independent variables, and male behaviour, e.g. date when a male started building its nest, and reproductive success as response variables (Table 2). If we assume that the first returning Penduline Tit occupies the higher quality territories first, then one expects a negative association between the PCs and date of nest-building (Aebischer *et al.* 1996, Currie *et al.* 2000, Eckerle & Thompson 2006).

To avoid pseudoreplication, only one randomly selected nest of colour-ringed males was included in the dataset – except in the analyses of nest building when the first nest of each individual male was included – and the composition of pairs was always different, unless otherwise stated. Unringed males were excluded from the analyses. A potential effect of pseudoreplication of nest-sites cannot be excluded. However, given the sample sizes for each separate test and the fact that the data originate from two years, this effect is likely to be small. Moreover, several nests are rarely built in exactly the same nest-site, i.e. the same tree, within a year (R.E. van Dijk & I. Szentirmai, pers. obs.). Between years this is possible, but habitat structure is likely to change for a given nest-site at a given time in the season between years. Data on mating time were normalised using a log(x+1) transformation. Analyses were performed using SPSS 14.0.0 for Windows. We provide mean ± SD.

RESULTS

Habitat structure influenced the date males started nest building at a given nest-site (Table 3). This was mainly accounted for by PC1 (Fig. 1), suggesting that habitats containing a larger number of Poplars are selected first by males. The slopes for PC1, PC3 and PC4 were negative (regression coefficients B = –12.398, –2.622, and –0.446, respectively). The slope for PC2 was positive (B = 0.139). Although the individual effects of PC2, PC3 and PC4, were not significant ($P > 0.232$), overall, nest-sites were occupied earlier with increasing values for habitat structure.

Table 3. Regression ANOVAs investigating the effect of habitat structure (expressed as four PCs; see Table 1) on date of nest-building initiation, male mask size, mating time and reproductive success. Separate models were created for each response variable to maximise sample sizes (see Table 2).

	F	*P*
Date of nest initiation	4.858	0.002
Male mask size	0.391	0.814
Mating time	1.080	0.379
Number of eggs	0.463	0.762
Number of chicks	1.077	0.390
Hatching success	1.096	0.378

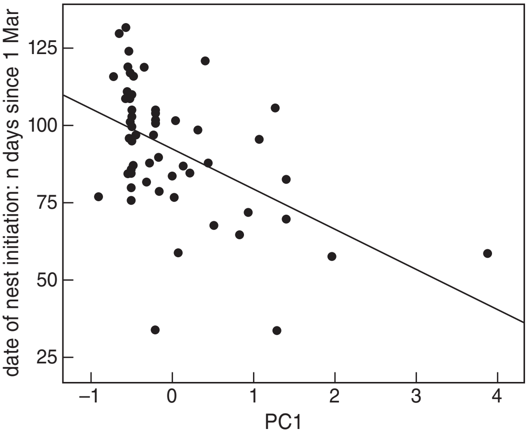

Figure 1. With an increasing PC1, mainly accounted for by the number of Poplars, nest-sites were occupied earlier in the season (Least Squares Regression; regression coefficient B = –12.921, $F_{1,54} = 18.483$, $R^2 = 0.255$, $n = 56$ nests, $P < 0.001$).

Habitats with a higher vegetation density were not occupied by more attractive males (Table 3), which have larger mask sizes (Kingma *et al.* unpubl. data). Also, habitat structure did not predict reproductive success, as measured by the number of eggs at the eighth day after start of incubation, the number of nestlings at the tenth day after hatching, and hatching success calculated as the percentage of offspring that survived from egg to 10-days old nestling (Table 3).

At 114 out of 187 nests included in this study across two years the male attracted a female to its nest and egg-laying was initiated (2004: 36 out of 48 nests, 2005: 78 out of 139 nests). We did not find any effect of habitat structure on mating time (Table 3), nor on mating success (Table 4A).

None of the habitat structure variables predicted whether (a) the female or (b) the male was more likely to care or desert (Table 4B and 4C).

DISCUSSION

Consistent with our predictions, we show that habitats consisting of a denser vegetation structure in the immediate surroundings of the nest were occupied earlier in the season. Similar results have been reported for other bird species (Aebischer *et al.* 1996, Currie *et al.* 2000, Eckerle & Thompson 2006). However, habitat structure did not affect reproductive success of Penduline Tits (see also Darolová & Hoi 1996), nor did it influence the outcome of sexual conflict over nestling provisioning in our study population. The latter result contradicted our expectations: we would expect that the relatively small male-only cared clutches require less food than the larger female-only cared clutches. We would therefore expect more male care in habitats with less suitable vegetation (Krištin 1995). However, the difference in number of nestlings between male- and female-only cared clutches was not significant (2.7 ± 1.1 nestlings for male-only (n = 7 nests) vs. 3.8 ± 1.5 nestlings in female-only (n = 7, 39 nests, respectively); Mann-Whitney U = 79.50, P = 0.074). This non-significant difference in number of nestlings may partly explain why Penduline Tits did not adjust clutch size and type of parental care (male-care, female-care or biparental desertion) to habitat structure, given that the nestling-phase is when food availability is likely to be most crucial in Penduline Tits (Bleeker *et al.* 2005). However, it should be noted that the sample size for male-only cared nests was small and that the difference in number of nestlings was close to significance. Also, although there was some variation in hatching success (Table 3), there was no effect of habitat structure on hatching success. This suggests that food was sufficiently available for larger broods being raised by one parent only. The variation in hatching success may have been due to other factors than habitat structure, such as parental qualities. Nestling survival, calculated as percentage of nestlings that survived from day of hatching till ten days after hatching, is high in our population (78.7% ± 24.3, R.E. van Dijk, I. Szentirmai, T. Székely, unpubl. data). This again suggests that food is generally sufficiently available. These results on reproductive success vs. habitat structure are consistent with the suggestion for Blue Tits *Cyanistes*

Table 4. Binary logistic regression models of (A) mating success (n = 70 nests), (B) female care strategy (n = 41 nests), and (C) male care strategy (n = 41 nests) in response to habitat structure. Desertion by the female is defined as female-only desertion and biparental desertion; similar for desertion by male. In both models care was labelled '0' and desertion '1'. All models adequately fit the data (Hosmer-Lemeshow goodness-of-fit; (A) χ^2 = 6.217, df = 8, P = 0.623; (B) χ^2 = 2.615, df = 8, P = 0.956; (C) χ^2 = 14.979, df = 8, P = 0.060). Predicted effect sizes and standard errors are given.

	Model effect estimate (± SE)	Wald	*P*
A Mating success			
PC1	–0.243 ± 0.236	1.062	0.303
PC2	0.405 ± 0.366	1.227	0.268
PC3	–0.029 ± 0.283	0.010	0.919
PC4	0.108 ± 0.300	0.129	0.719
B Female care strategy			
PC1	–0.032 ± 0.478	0.004	0.947
PC2	0.100 ± 0.328	0.093	0.761
PC3	1.476 ± 2.709	0.297	0.586
PC4	–0.555 ± 0.386	2.073	0.150
C Male care strategy			
PC1	–0.537 ± 0.525	1.048	0.306
PC2	–0.231 ± 0.345	0.449	0.503
PC3	–0.404 ± 0.424	0.909	0.340
PC4	0.435 ± 0.502	0.752	0.386

caeruleus that food limitation during the nestling period might not be the primary force shaping the reproductive output, and that in food rich habitats potential effects on reproductive success are much less pronounced (Tremblay *et al.* 2003).

We did not find an effect of habitat structure on either mating success or mating time. A line of arguments similar to that described above for reproductive success and provisioning may be followed here. If food and nest material is *generally* very abundant, then a male in a vegetation rich habitat will not have a pronounced mating benefit over a male in a habitat with slightly less vegetation. The idea of generally abundant food and nest material resources fading out a potential effect on mating success and breeding biology is supported by the fact that uniparental care appears to be sufficient for the survival of the offspring and by the low territoriality of the species. However, other possible explanations for our failure to find an effect of habitat structure on the Penduline Tit's breeding biology should not be excluded. For instance, (i) food and nest material availability may vary among habitats with similar vegetation structure. A more direct quantification of food and/or nest material availability may find support for our hypotheses. (ii) We did not find an effect of habitat structure on the breeding biology of Penduline Tits within one population. It may be interesting to compare populations breeding at different sites, with a potential for larger variation in habitat structure.

Although we did not find any influence of habitat structure on the breeding system of Penduline Tits within the two years of study, on an evolutionary timescale the impact may have been prominent (Davies *et al.* 1995). Although we do not have precise measurements on food availability, food in our study area seems to be generally abundant (R.E. van Dijk, I. Szentirmai, and T. Székely, pers. obs.). Such a high food availability may have promoted the evolution of sexual conflict over care provisioning and subsequent polygamy in this species (Davies 1991, Andersson 2005), since it will facilitate the survival of offspring with uniparental care only. Incidentally, a closely related species of the Eurasian Penduline Tit, the Cape Penduline Tit *Anthoscopus minutus* (Sibley & Ahlquist 1995), lives in a poorer habitat, the South African 'fynbos', and it exhibits facultative cooperative breeding, radically different from the Eurasian Penduline Tits (R.E. van Dijk and T. Székely, pers. obs.). In the future it will be interesting to carry out phylogenetic comparative analyses among closely related species, e.g. including Remizidae and Paridae, to investigate the influence of habitat structure on breeding system evolution. Using a detailed phylogeny one may be able to distinguish between two evolutionary trajectories: (i) sexual conflict evolved in food rich habitats, or (ii) species exhibiting sexual conflict spread into food rich habitats. Together with case studies such as the one we present here, this may help to unravel the causes behind variable breeding systems at different taxonomic levels (Davies *et al.* 1995). Furthermore, experimental manipulation of food and/or nest material availability will be a more direct approach to test its importance in resolving sexual conflict over care.

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SAMENVATTING

De verdeling van bronnen, zoals een ruimtelijke of temporele verdeling van voedsel, is dikwijls van invloed op reproductiesystemen. Een dergelijke invloed is vooral relevant voor soorten met een variabel broedsysteem. Wij hebben zo'n soort bestudeerd, de Buidelmees *Remiz pendulinus*. Deze kleine zangvogel vertoont opeenvolgende polygamie door beide seksen. Bewijs uit eerdere studies suggereert het bestaan van een intens conflict tussen beide seksen over ouderlijke zorg. Ouderlijke zorg wordt slechts door één van beide ouders op zich genomen, hetzij door de man, hetzij door de vrouw, terwijl ongeveer 30–40% van de legsels door beide ouders kan worden verlaten. Wij hebben de structuur van de habitat vastgesteld door de vegetatie die voor het foerageren en de nestbouw van belang wordt geacht te zijn, te scoren binnen de directe omgeving van het nest. Gebruikmakend van vier principale componenten laten we allereerst zien dat habitats met een dichte vegetatie eerder worden bezet dan habitats met een spaarzame vegetatie. Echter, de structuur van de habitat is niet van invloed op het paringssucces, noch op het reproductief succes. Ook kan aan de hand van de habitatstructuur niet voorspeld worden welke van de beide ouders (de man, de vrouw of beide) het legsel zal gaan verlaten. We stellen dan ook dat habitatstructuur geen direct effect heeft op het reproductief succes, noch op de uitkomst van het conflict tussen de seksen in Buidelmezen. De mogelijke invloed van specifieke eigenschappen van een habitat, zoals de beschikbaarheid van voedsel of nest materiaal, zal nog nader onderzocht moeten worden. Echter, op een evolutionaire tijdsschaal zou een algemeen hoge beschikbaarheid van voedsel en nestmateriaal mogelijk een belangrijk effect gehad kunnen hebben: het is niet ondenkbaar dat de evolutie van het voor vogels ongebruikelijke broedsysteem van Buidelmezen er door bevorderd is.

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