

Differences in song repertoire size and composition between two populations of blue tit *Parus caeruleus*

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We recorded songs of male blue tits *Parus caeruleus* during the fertile and egg-laying period in a Belgian and Spanish population and compared several song characteristics in order to investigate the extent of macrogeographic variation in song features such as syntax, repertoire size and the proportion of trills in the repertoire. Repertoire size differed considerably between populations: it was twice as large in southern Spain (11.6 song types) as in Belgium (5.4 song types). Song syntax also differed significantly between the two populations. The most remarkable difference, however, was found in the proportion of trills. Trilled song types were rare in southern Spain (18 %) whereas more than half of the song types in the repertoire of Belgian blue tits included a trill (53 %). A recent hypothesis explains variation in blue tit song as a result of interspecific competition, suggesting that blue tit repertoire size decreases with increasing density of great tits *Parus major* and that the proportion of trills increases with increasing great tit density. This hypothesis does not appear to explain our findings. Although both populations differed strongly in both song parameters, the relative great tit density appeared to be very similar. Furthermore, we provide the first evidence of a striking negative relationship between repertoire size and the proportion of trills in the repertoire. Thus, birds with a large repertoire tend to have only a small proportion of trills, whereas birds with a small repertoire usually have a large proportion of trills.

Key words: Blue tit song, geographic variation, *Parus caeruleus*, *Parus major*, song repertoire, repertoire size, trills.

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The analysis of geographic variation in bird song has been used to examine mechanisms of song development (Marler & Pickert 1984), the process of cultural evolution (Lynch & Baker 1993) and the different functions of song forms (Rothstein & Fleischer 1987). Geographic variation can be expressed in many song features. Average repertoire size, for example, can vary geographically among populations of the same species (Kroodsma & Canady 1985). In blue tits *Parus caeruleus*, repertoire size (the number of different song types per individual) differs noticeably among populations. Bijmens and Dhondt (1984) found an average repertoire size of 5.25 song types in their Belgian population whereas French and Corsican blue tits possessed

on average three and four different song types respectively (Doutrelant et al. 2000a). In contrast, the mean repertoire size of a blue tit population in La Gomera, one of the Canary Islands, was 19 different song types (Schottler 1995).

The syntax of blue tit song also shows great variation from northern Europe to the Mediterranean region, North Africa and the Canary Islands. In northern Europe, blue tits frequently sing trills (Fig. 1), a series of rapidly repeated notes in the last subphrase of a strophe (Becker 1980, Bijmens & Dhondt 1984, Doutrelant & Lambrechts 2001), whereas no trills have been reported in North Africa and the Canary Islands (Becker 1980, Schottler 1995). As for other life history

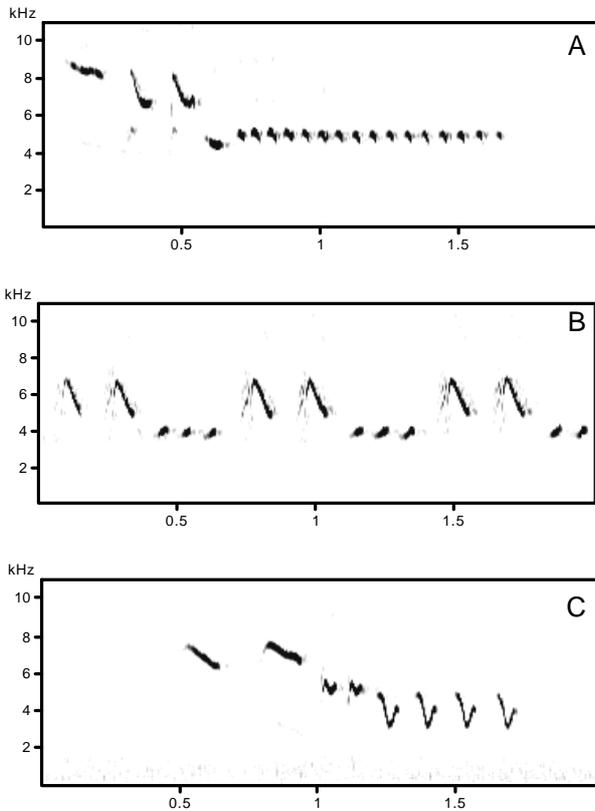
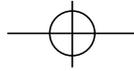


Figure 1. Example of (A) a trilled, (B) untrilled, and (C) intermediate blue tit song type. A trill is a series of identical notes in the last subphrase of a strophe, rapidly repeated in a sequence. The last subphrase of an intermediate song type also consists of identical notes, but it is characterised by a very short sequence and a slow repetition of notes.

traits (Blondel et al. 1993), repertoire size and the incidence of trills might have evolved in response to geographic variation in local selection pressures.

Interspecific competition has been suggested to be one of the major evolutionary forces responsible for population differences in ecological, morphological, physiological and behavioural characteristics (Brown & Wilson 1956, Grant 1972, Schluter 1994). Recently, Doutrelant et al. (2000b) have proposed that blue tit repertoire size and the proportion of blue tit trilled song in the repertoire are related to the level of interspecific competition with a close competitor, the great tit *Parus major* (Character Shift Hypothesis; Doutrelant et al. 2000b). Since both species are able to produce

sounds with a similar syntax and frequency range, acoustic competition between these species could have caused a shift in blue tit song syntax. By using trills (of different syntax), blue tits can avoid the problem of being misidentified by great tits and therefore trilled song might reduce the probability of energy-demanding, aggressive territorial interactions with the more dominant great tits (Doutrelant et al. 2000b; Doutrelant & Lambrechts 2001). A recent study of the phylogeny of the Paridae confirms the fact that these two species are close relatives, i.e. sister taxa in a monophyletic group that is the sister taxon to all other parids (Slikas et al. 1996). Furthermore, both species occupy the same habitat, breed during the same period in overlapping territories and compete for food and nesting cavities (Dhondt 1977, Török & Tóth 1999).

In this study, we tape-recorded blue tits in a population in southern Spain and compared song types and song characteristics with data from a Belgian population. We also investigated the relationship between relative great tit density, blue tit repertoire size and the proportion of song types sung with trills in the Belgian and Spanish populations. Within each population, we also examined whether there is a correlation between individual repertoire size and the proportion of trills. Assessment of these findings may shed new light on the evolutionary driving forces behind the large geographic variation in blue tit song features.

Methods

Study areas

In Belgium, the study area was part of the campus of the University of Antwerp (UIA) and the recreation and nature reserve Fort VI in Wilrijk-Edegem (51°10'N, 4°25'E; see also Van Duyse et al. 2000). The entire area has been provided with nest boxes since 1996. The dominant tree species are deciduous. The study area in southern Spain has been provided with nest boxes since 1999. Benahavis (36°31'N, 5°02'W) is a small mountain village near Marbella and is mainly surrounded with small and large fragments of pine *Pinus* sp. and cork oak *Quercus suber* woodland. Blue tits in Belgium and southern Spain belong to different subspecies (*P. c. caeruleus* and *P. c. ogliastreae* respectively) and this is mainly reflected in the body size, with *P. c. ogli-*

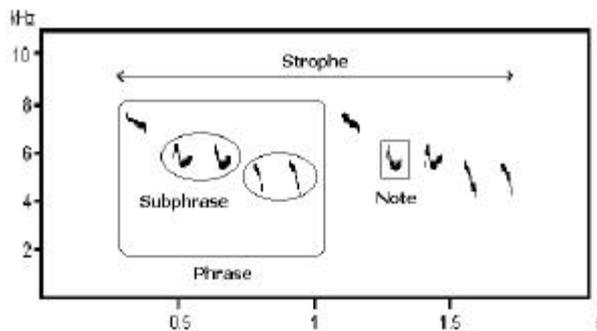
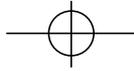


Figure 2. Sonogram of an untrilled song type of a Spanish blue tit. The x-axis represents the time (s), the y-axis the frequency (kHz). A phrase is a group of notes that are stereotypically repeated. Each phrase can be divided into several subphrases of identical notes (in this case the phrase consists of 3 subphrases), which differ in frequency range. The whole set of stereotypically repeated phrases is a strophe.

astrae being a little smaller than *P.c. caeruleus* (Cramp & Perrins 1993).

Song recordings and parameters

Songs were recorded during the blue tits' fertile and egg-laying periods in the two study populations. In Belgium, dawn choruses from 15 colour-ringed males were recorded during March–April 1997. During the same period in 2000, dawn choruses from eight unmarked males were recorded in southern Spain. Individual males in Spain could be easily distinguished because their singing perches were widely separated. Most individuals were recorded on a single morning (complete dawn chorus) because this gives a good estimate of the individual repertoire size (see Doutrelant & Lambrechts 2001). All recordings were made using a Sony WM-D3 cassette recorder or a Sony MZ-R90 minidisc, which was connected to a Sennheiser ME 67 microphone. Songs were analysed using the Avisoft SASlab Pro software (20 kHz sampling rate; antialiasing filter; Hamming window type) and a ESS AudioDrive Record (1000) 4.7 soundcard (16 bit).

Parameters measured per male were: (1) repertoire size, (2) mean strophe number, (3) mean note number, (4) mean minimum frequency, (5) mean maximum frequency, (6) mean frequency range and (7) the proportion of trilled, untrilled and intermediate song types

(Fig. 1). Strophe number is the number of repetitions of the same song type that a bird sings before switching to another song type (Fig. 2). Note number is the number of different notes used per song type. Frequency measures and note numbers were quantified using one representative strophe per song type and calculating the mean of these values per individual. Trilled song types contain a long series of identical notes in the last subphrase of a strophe, rapidly repeated (less than 60 ms between two notes) in a sequence (see Doutrelant et al 1998). Intermediate song types are characterised by a very short and slow repetition (more than 60 ms between two notes) of identical notes in the last subphrase (Fig 1). To determine the proportion of trilled song types in each study area, we calculated the proportions of trills for all the recorded males.

When comparing results of different studies of the same species, one should take into account the possibility that methods for defining and counting song types may differ across studies (Peters et al. 2000). Although some level of subjectivity can occur in defining song types in blue tits, this is very unlikely since variation within song type is very low in this species and songs of both the Spanish and Belgian population were analysed by the same person.

Relative density estimations

In Belgium, relative great tit density was estimated as the number of breeding great tits divided by the combined number of breeding blue and great tits. Because nest box occupation was low in the study area in southern Spain, we were not able to estimate the relative great tit density in this way. Instead, we estimated relative great tit density as the number of great tits detected (singing a dawn chorus), divided by the number of detected blue and great tits (Doutrelant & Lambrechts 2001). As the study area in southern Spain was only about 20 ha in size, singing blue and great tits were easily discovered. Singing activity at dawn was gathered on three different mornings (17 March, 30 March, 13 April) by following a transect through the study area and noting the number of singing blue and great tits. We think this method gives a reliable estimate of relative great tit density because both great and blue tits are equally detectable during the dawn chorus, we obtained similar values for relative density on different days and the average value is comparable to that found in seven

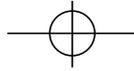


Table 1. Song characteristics of blue tits recorded during the dawn chorus in Benahavis (southern Spain) and Antwerp (Belgium). Values reported are means \pm s.e.

Mean \pm s.e.	Spain	Belgium	df	t-value	P-value
Repertoire size	11.62 \pm 0.88	5.40 \pm 0.44	21	7.05	0.000001
Strophe number	55.45 \pm 9.62	32.60 \pm 4.51	21	2.46	0.023
Note number	2.66 \pm 0.12	2.74 \pm 0.12	21	-0.45	0.65
Minimum frequency (kHz)	3720 \pm 66	4255 \pm 69	21	-4.97	0.000063
Maximum frequency (kHz)	8118 \pm 95	8262 \pm 90	21	-1.01	0.32
Frequency range (kHz)	4398 \pm 90	4007 \pm 106	21	2.42	0.025

ral other nest box populations in similar habitat types in southern Spain (J. S. Monros, pers. comm.).

Statistical analyses

Statistical analyses were performed using Statistica for Windows (1994). Data were checked for normality before performing parametric tests (Student t-test), transformed if necessary and, if still non-normally distributed, nonparametric statistics (Mann-Whitney U-test) were used. Spearman rank correlations were calculated for the relationship between repertoire size and the proportion of trilled song types. Values reported are means \pm s.e.

Results

In total, 33 different song types were distinguished in the Belgian population from recordings of 15 males. In Benahavis, 47 different song types were recorded during the dawn chorus of eight males. Blue tits in Belgium had only three song types in common with blue tits in Spain. In Belgium, relative great tit density, calculated as the number of breeding birds, was 0.50 at the time of recording. In southern Spain, average relative great tit density, calculated as the number of detected birds on three different days, was 0.57 ± 0.002 at the time of recording.

Repertoire size

Blue tits in Spain had on average twice as many song types in their repertoire compared to Belgian blue tits (Table 1, Fig. 3). Repertoire size varied from 7 to 15 in

Spain and between 3 and 8 in Belgium. With the exception of one individual in Spain, there was no overlap in repertoire size between the two populations. The difference in repertoire size between Spanish and Belgian blue tits was highly significant (Table 1).

Song syntax and the proportion of trills

Blue tits from Spain sang a given song type significantly more before switching to the next than did Belgian blue tits (Table 1). The variation between individuals, however, was quite high. In Belgium, one bird sang on average only 12 strophes of one song type before switching to another song type, whereas another blue tit sang on average 69 strophes. In Spain, the range in strophe number varied from 22.1 to 94.5 strophes.

No significant differences were found between Belgian and Spanish blue tits in the mean maximum frequency or in the number of different notes per song type. In contrast, the mean minimum frequency in Spain was significantly lower than the mean minimum frequency in Belgium (Table 1). The frequency range, consequently, appeared to be significantly larger in Spain.

The song repertoire of a blue tit in southern Spain contained on average 18 % trilled song types (range 0 % to 29 %; Figs. 4 and 5). In Belgium, a repertoire contained on average 53 % trilled song types (range 20 % to 100 %; Mann-Whitney U = 4.0; P < 0.001).

Further, the syntax of trilled songs appeared to be different in Belgium and Spain. Approximately 42 % of the trilled song types in Spain consisted of four subphrases, whereas trilled song types containing four subphrases were never recorded in the Belgian population (Fig. 1). This difference was highly significant

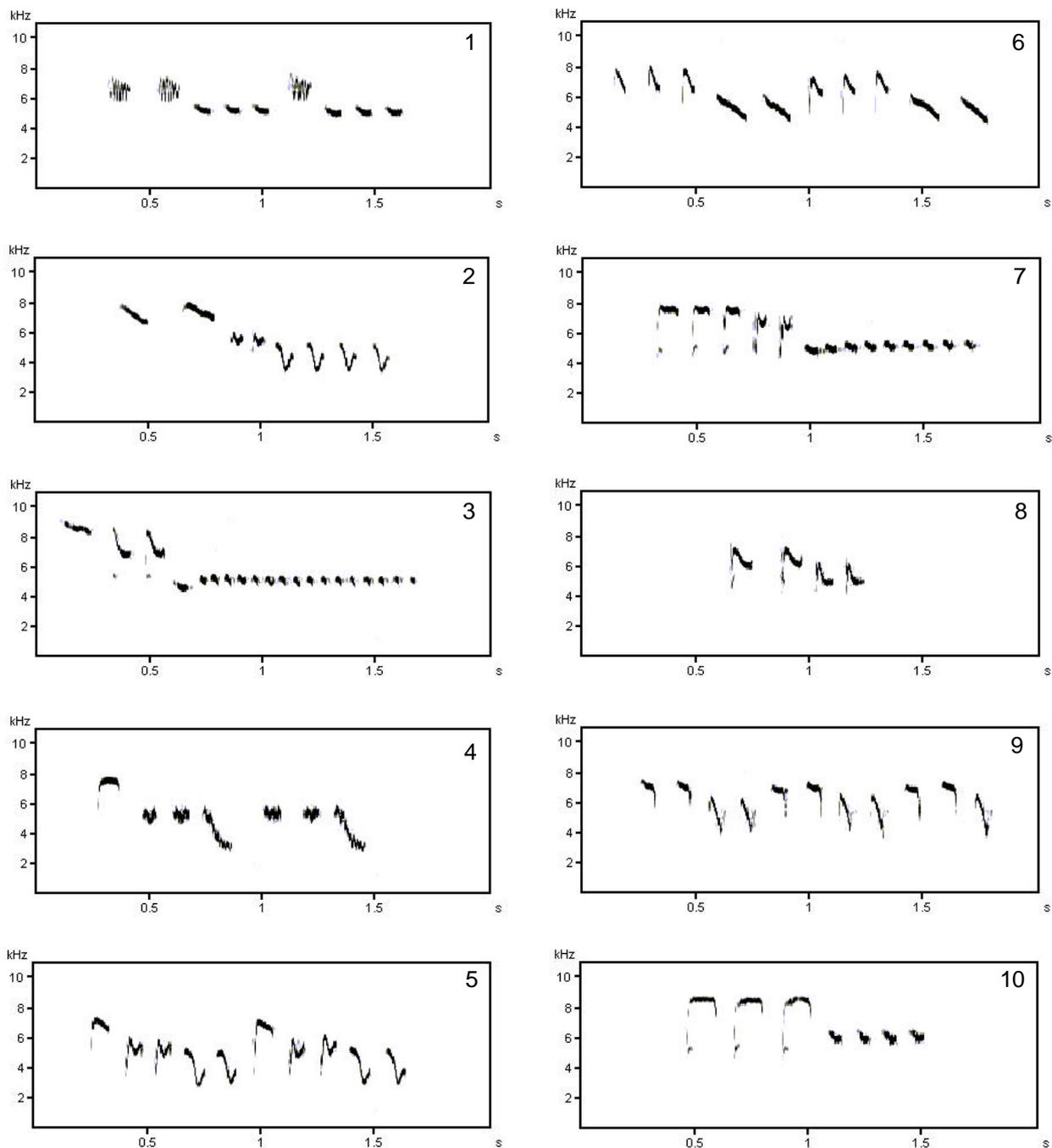
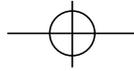


Figure 3. Example of a blue tit repertoire in southern Spain. Repertoire size of this individual was 10. Numbers 1, 4, 5, 6, 8 and 9 are untrilled song types, 3 and 7 are trilled song types and numbers 2 and 10 are intermediate.

(Mann-Whitney $U = 8.0$; $P < 0.001$). On the other hand, Belgian blue tits sang proportionally more trilled song types of three subphrases than their Spanish conspeci-

tics (89 % versus 23 %; $U = 4.5$; $P < 0.001$). The proportion of song types with a trill in the second subphrase did not differ between the two populations ($U = 48$; $P >$

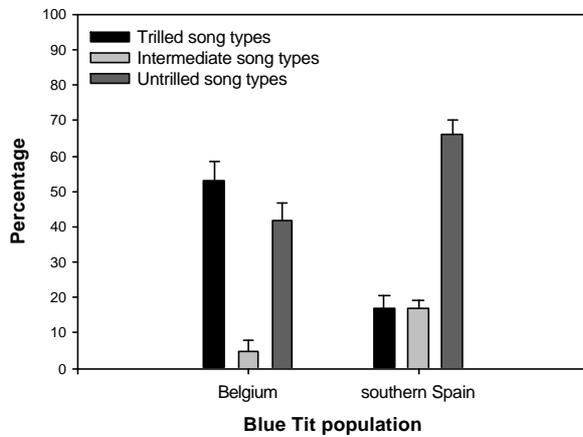
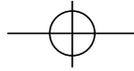


Figure 4. The proportion of trilled, untrilled and intermediate song types (\pm s.e.) in the repertoires of Belgian and Spanish blue tits which were recorded during their dawn chorus.

0.05). Significantly more intermediate song types occurred in the Spanish population (17 % versus 6 %; $U = 22.0$; $P = 0.01$).

Correlation between repertoire size and the proportion of trills

There was a significant negative correlation between repertoire size and the proportion of trills in Belgium (Spearman rank; $n = 15$; $r_s = -0.59$; $P < 0.02$; Fig. 5). In Spain, the correlation between repertoire size and proportion of trills was also negative and approached significance (Spearman rank; $n = 8$; $r_s = -0.68$; $P = 0.06$).

Discussion

Repertoire size

Blue tit song characteristics differ considerably between Belgium and southern Spain. First, the mean repertoire size in Spain is twice as large as the repertoire size in Belgium. In comparison with repertoire sizes found in other study sites, these found in southern Spain are remarkably large. Only in Gomera (Canary Islands) are repertoire sizes even larger (Schottler 1995). Although it has not been tested rigorously, it is at present assumed that recording a complete dawn chorus gives

a good estimate of an individual's repertoire size (see also Doutrelant & Lambrechts 2001). The repertoire size obtained in our Belgian population (5.40 song types) was very similar to that reported by Bijmens and Dhondt (1984) in another Belgian population (5.25 song types). The fact that, in Corsica, blue tits of the same subspecies (*P. c. ogliastrae*) as in southern Spain have on average only 3.2 different song types in their repertoire (Doutrelant et al. 1998) indicates that such macrogeographic variation represents more than a subspecies effect.

We can only speculate as to why repertoires in the Spanish population are twice as large as repertoires in Belgium. First, the larger repertoires found in Spain could be associated with the likelihood of year-round

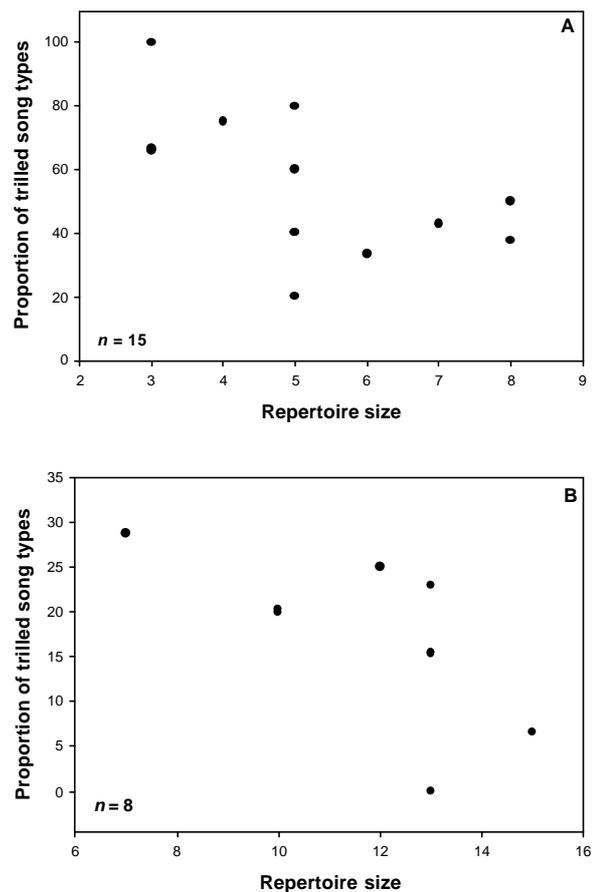
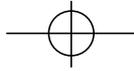


Figure 5. Relationship between repertoire size and the proportion of trilled song types of blue tits in (A) Belgium and (B) southern Spain. Each point represents an individual male.



territoriality instead of territoriality only during the fertile and breeding period in northern Europe (Kroodsmas & Canady 1985, Kroodsmas & Verner 1987). Second, one could ascribe the larger repertoires in Spain to the possibility that, due to constraints in visual communication, acoustic communication is more predominant in closed evergreen habitats than in open deciduous habitats (see also Brown et al. 1995). Finally, variation in repertoire size between populations of the same species may be related to variation in the intensity of sexual selection or population density (Catchpole 1980, Kroodsmas 1996).

Frequency parameters

Frequency parameters also differed between the two populations. Differences in frequency are often ascribed to factors related to sound transmission (Morton 1975, Hansen 1979, Wiley & Richards 1982). High frequencies degrade more rapidly in dense vegetation (Wiley & Richards 1982), so that birds inhabiting open habitats tend to produce sounds of higher frequencies compared to birds in dense vegetation. Unlike deciduous habitats, the vegetation in evergreen habitats remains dense all year round, especially in early spring, when singing activity peaks. This could explain the fact that Spanish blue tits inhabiting dense evergreen vegetation, on average use a lower minimum frequency than Belgian blue tits inhabiting deciduous woodland.

Proportion of trills and intermediate song types

Spanish blue tits sang significantly fewer trilled song types and significantly more intermediate song types than their Belgian conspecifics. Untrilled and intermediate song types could be an adaptation for transmission in evergreen vegetations. As fast amplitude modulations (trills) degrade more rapidly in dense vegetations, rapidly repeated notes soon become indistinguishable to the listener as the inter-element spaces fill with echoes (Wiley & Richards 1982). Hence, untrilled and intermediate song may be better suited than trilled song for transmission in a closed habitat (Brown & Handford 2000) and this could possibly explain the small proportion of trills found in the Mediterranean region. However, results of an experimental study by Doutrelant et al. (1999) suggested that trilled and untrilled song are both efficient for communication in the dense vege-

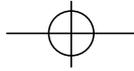
tation of their French and Corsican study plots. They showed that blue tits reacted equally strongly to degraded trilled and untrilled song.

Macrogeographic variation in the proportion of trills

Preliminary song recordings made after stimulation (playback) in Benahavis and in a second study area in Ojén, approximately 60 km from Benahavis, showed that the distribution of trilled, untrilled and intermediate song types appeared to be very similar (Mann-Whitney U-test; all P-values > 0.05), suggesting that these song characteristics are representative for a larger area in southern Spain.

The question of why trills are rare in the Spanish population is not easy to address. Recently, trills have been suggested to be the result of a character shift in blue tit song caused by interspecific competition with the more dominant great tits (Doutrelant & Lambrechts 2001). According to Doutrelant & Lambrechts (2000b), the proportion of trills in the repertoire is correlated with the relative breeding density of great tits and is not correlated with other environmental factors such as vegetation characteristics or blue tit density. They found a high relative density of great tits in southern France (0.60) and Denmark (0.55), where blue tits frequently sing trilled songs (65 % in France and 75 % in Denmark) and a rather low great tit density in Corsica (0.35), where blue tit song repertoires consist only or mostly of untrilled song types (mean percentage of trills 23 %). Furthermore, Doutrelant et al. (2000a) also suggested that the number of song types per individual blue tit might decrease with increasing great tit density. Consequently, the exceptionally large repertoires in Gomeira on the Canary Islands could be explained by the fact that great tits are absent on these islands and therefore that sexual selection is not counterbalanced by interspecific competition.

These hypotheses do not appear to explain our findings because relative great tit density in the Spanish and Belgian population appeared to be very similar (0.57 in Spain and 0.50 in Belgium), whereas repertoire size and the proportion of trills were clearly very different. However, we cannot rule out the Character Shift Hypothesis completely because micro-habitat use may differ between the two tit species in the Spanish population, and second, although the relative great tit



density is high, absolute great tit density may be low, reducing the level of interspecific competition in the Spanish plot.

Correlation between repertoire size and the proportion of trills

Our data show that birds with a large repertoire tend to have only a small proportion of song types containing a trill, whereas birds with a small repertoire usually have a large proportion of trilled song types. This negative relationship between repertoire size and the proportion of trills is at present not easy to interpret. It may imply that if blue tits can enlarge their repertoire size, they 'prefer' to choose only or mostly untrilled song types. This could be due to some unknown constraints on performance and, since some studies on great tits have revealed a correlation between repertoire size and male quality (Lambrechts & Dhondt 1986, Lambrechts & Dhondt 1987), it might be possible that blue tits of low quality have more difficulty in producing untrilled song. Otherwise, females could prefer untrilled song and/or untrilled song could be an advantage in male-male interactions. On the other hand, it can also imply that blue tits with a small repertoire prefer to learn trilled song types. Indirectly, this may indicate that trilled song may serve as the basic communication required to obtain a mate and a territory (intra- and inter-sexual communication).

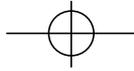
Our results suggest that there are other unknown factors that influence the proportion of blue tit trilled song and repertoire size. Factors such as acoustic adaptation, energetic and morphological constraints, variation in female choice and juvenile learning preferences need to be examined in the future, in order to reveal the extent to which each contributes to the large geographic variation in blue tit song features observed today.

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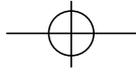
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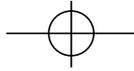


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Agonistic encounters among willow tits *Parus montanus* with emphasis on vocalisations and displays

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The study was carried out in the alpine birch region in Ringeby in central Norway from 1987 to 2000. All encounters between willow tits *Parus montanus* with aggressive elements were noted and many were tape- or video-recorded. Both adults and juveniles took part in such encounters, which were probably involved in the establishment of social hierarchies, pair formation, territorial claims or food competition. The number of participants varied from two to about ten individuals. Encounters were usually accompanied by much vocalisation, pursuit, attacks and sometimes combat with physical contact. Males took part in agonistic encounters much more often than females. The most common utterings were gargles, *tää* (or *si-tää*) calls, *pjä* (or *dsjä*) calls, *zizi* and *spitt* alarm calls, all of which appear to express aggression, alertness or excitement. Song, if at all used, was mostly heard just before or after the encounters. Combat resulting in injuries was never observed. The number of gargles given increased significantly with increased aggression. Different types of displays during encounters, including wing-flicking, are described and their functions suggested.

Key words: willow tit, *Parus montanus*, agonistic display, vocalisation.

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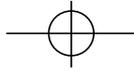
Intraspecific agonistic encounters take place commonly in the daily life of titmice *Parus* spp. The severity of fighting varies greatly, expressing a continuum from very brief encounters without any physical contact between the participants to fierce but brief physical combat. A whole spectrum of calls is usually uttered during such encounters, depending on the number of birds involved. The participants may number up to about ten individuals, not at all of which are involved in the skirmish with equal intensity. Violent fights including physical contact occur less commonly and seldom if ever lead to injuries. Most encounters are just vocal events with mutual movements and pursuits. They may last from a few seconds to several minutes. Although agonistic encounters in tits are frequently observed in nature, the vocalisations used do not seem to have been fully described in any *Parus* species. In this paper I describe the behaviour of the willow tit *Parus montanus* during such encounters.

Material and methods

The data were collected as part of a long-term study of the general biology of willow tits in the alpine birch region at Venabu (61°39'N, 10°08'E) in Ringeby municipality, central Norway, during the period 1987–2000.

More than 560 agonistic encounters were observed of which 136 were sound-recorded, using a Sony TC-D5 Pro recorder fitted with a parabolic microphone (Telinga Pro III). Analyses of the recorded vocalisations were made using a Uniscan FX-85. Additionally I made video recordings at feeding tables, using Hi8 cameras (Sony or Hitachi).

Most birds were individually colour-ringed and their sex and age were determined by the methods described in Haftorn (1997). However, quite a few juveniles that immigrated to the study area in late summer and autumn were observed in encounters before I managed



to catch them. Thus, some encounters considered here involved unringed birds.

All encounters with aggressive components were noted, whether they occurred in connection with feeders or not. Many conflicts were observed when single birds or flocks came into contact when roaming about in the study area. Aggressive encounters already occur among fledglings in the natal territory when the young are still dependent on their parents (Haftorn 1997). Encounters among siblings during this phase are omitted in the present paper, which includes only encounters among independent juveniles and adults. Because I could not find any difference in behaviour between conflicts at feeders and away from feeders all the data were combined for further analyses.

An encounter is defined as a meeting between at least two individuals in which elements of aggressiveness are involved. A combat is an encounter in which attacking birds have physical contact with each other. Conflicts between individuals are usually easily detected by man because of the intensity of vocalisations, but less serious encounters may be carried out in silence.

Age of participants

Four main types of aggressive encounters may be recognised according to the composition of the parties involved:

1. Encounters between juveniles: During the period of dispersal, juveniles gather temporarily in flocks (Haftorn 1997). Meetings between single juveniles or juvenile flocks often lead to encounters that evidently are associated with pair formation, establishment of social hierarchies or possibly the foundation of winter territories. Encounters of this type were frequently observed from July to September.

2. Encounters between juveniles and adults: Formation of winter flocks involves meetings between juveniles and territorial adults. Such encounters in late summer and early autumn may be of survival value to juveniles and are described elsewhere (Haftorn 1999).

3. Encounters between adults: Meetings between territorial adults often cause aggressive encounters.

4. Encounters between birds of mixed age: When established winter flocks meet they usually behave aggressively towards each other with much vocalisation.

Results

In the study area agonistic encounters usually took place in the upper parts of birch trees. Generally the birds involved moved relatively slowly towards the top, jumping from branch to branch with the subordinate in front and the dominant close behind. Having reached the treetop the subordinate would fly to a neighbouring tree tightly pursued by the dominant. In this way the birds often moved back and forth between trees for some time until the situation calmed down and the birds separated. Occasionally the two main opponents (usually males) clashed in the air and fell interlocked to the ground where they sometimes continued fighting for a few seconds before separating. The whole event was characterised by intense vocalisations from the participants. Such an encounter may be performed in 'waves' with peaks of intense aggression and much vocalising with intervals of markedly less aggression and vocalisation.

Agonistic meetings between willow tits did not always result in immediate quarrelling. There was often an initial phase in which the two parties seem to evaluate each other. During this phase the birds remained hesitant and silent and might sit more or less motionless before the encounter suddenly escalated.

Males were much more often engaged in agonistic encounters than females: of 84 encounters witnessed, males were involved in 70 and females in 39. Typically, in a conflict between two pairs the females were more reserved and contented themselves with various utterings, leaving the more hostile activities to their mates. In encounters with more than four birds, usually two males played the lead and carried out attacks, pursuits and even combats, while the others contented themselves with vocalising more or less intensively.

Females may also attack one another, though more rarely. Typically, any males present during female quarrelling did not interfere. Female conflicts followed the same pattern as between males, but were usually less violent. Physical clashes in the air, which happened rather frequently between males, seldom if ever occurred between females.

Vocalisations

Table 1 shows the different vocalisations used in agonistic encounters among willow tits, for juveniles and

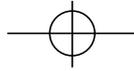


Table 1. Vocalizations given during agonistic encounters among willow tits. n = number of encounters, % = percentage of encounters with the call in question (e.g. gargles used in 33 of 61 encounters, i.e. 54 %). Total number of encounters investigated: juveniles = 61; adults = 30; and encounters in which both juveniles and adults were involved = 45.

	Juv.		Ad.		Juv. + Ad.	
	n	%	n	%	n	%
gargles	33	54	20	67	25	56
<i>tää</i> calls	33	54	16	53	33	73
<i>sisi</i> alarm calls	25	41	13	43	20	44
<i>spitt</i> alarm calls	17	28	9	30	22	49
<i>pjä</i> calls	26	43	15	50	21	47
staccato calls	22	36	11	37	26	58
song	13	21	9	30	6	13
<i>sie</i> flight calls	11	18	4	13	4	9
<i>trrr</i> twitter calls	5	8	1	3	1	2
high-low calls	2	3	6	20	4	9
<i>sit</i> foraging calls	3	5	1	3	15	33
other calls	13	21	5	17	30	67

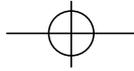
adults respectively. Independent of age the most common utterings were gargles (Fig. 1a–d), *tää* (or *si-tää*) calls (Fig. 2a–c), *pjä* (or *dsjä*) calls (Fig. 3a–b) and *zizi* alarm calls (Fig. 2d), all of which occurred in more than

40 % of the encounters recorded (Table 1). Less common were staccato calls (Fig. 1d), *spitt* alarm calls (Fig. 2c), song (Figs 3c, 4c) and flight calls (Fig. 3c). High-low (Fig. 3d) and *sit* foraging calls (Fig. 4a) were rather seldom heard. A special dry, snarling sound (*trrr*), here named twitter, was sometimes uttered (Fig. 4b) and probably expressed some kind of 'irritation' (see Haftorn 1997). Song, if used at all, was mostly heard just before or after the encounters, although it was sometimes integrated in the main dispute. Song introduced by one male occasionally developed into counter-song with another male.

The number of gargles increased significantly with increased aggression (Fig. 5). In particular, the number of gargles used in encounters with physical combat (class 6) was significantly greater than the number of gargles in non-combat encounters (classes 1–5; see text to Fig. 5; Mann-Whitney U-test, $U = 21.5$, 2-tailed $P = 0.007$). *Zizi* alarm calls also occurred most frequently during physical fighting (G-test, $P = 0.006$) and the same may be true of *spitt* alarm calls, though a G-test was not significant ($P = 0.065$). No other calls seemed to be related to increased aggression.

As previously described (Haftorn 1993) the *tää* calls varied a great deal in structure and combination with other calls. Rapid series of extra short *tää* notes (Fig. 2c) occurred fairly commonly in encounters between juveniles (used in 23 % of the encounters). In aggressi-

Figure 1. Different types of gargles given during agonistic encounters among willow tits: (a) adult male 21 August 1987; (b) 21 August 1987; (c) double gargle by an adult, 12 September 1987; (d) adult 7 July 1989, two elements of the staccato call preceding the gargle.



ve encounters between adults this call type was noted only once. Structurally these extra short *tää* notes are very similar to *spitt* notes; typical *spitt* notes often graded into short *tää* notes in the same call (Fig. 3c). A series of extra short *tää* notes probably expresses a high degree of excitement.

Displays

Aggression is shown by ruffling of the breast and back feathers, often combined with extended wings and fanned tail, a flattened crown and open bill (gaping). On the other hand, raised crown feathers signal submissi-

Figure 2. Calls during agonistic encounters among willow tits: (a) *tää* elements of relative long duration 13 September 1989; (b) *tää* elements of relative short duration 14 July 1991; (c) series of five *spitt* elements which grade into four extra short *tää* elements, ending with one prolonged *tää* element, given by a juvenile 10 July 1989; (d) *zizi* alarm signal, 22 July 1990.

Figure 3. (a–b) *Pjä* or *dsjä* calls given by two different juvenile willow tits, 14 July 1991 and 22 July 1990; (c) *sie* flight-calls above and song *tiuu* from two different adults, 15 August 1988; (d) high-low calls from an adult 15 August 1988.

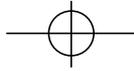


Figure 4. (a) *Sit* foraging call given by an adult willow tit, 25 May 1989; (b) twitter by a juvenile, 21 July 1989; (c) song *tiii* by an adult male, 8 July 1990.

veness. On three occasions I saw the single wing-flick display (sensu Smith 1996) being performed when two birds met at a feeding table (video-recorded). The dominant bird then instantly flicked one wing (left or right) vertically in the air and down again, and at the same time fanned the tail and flattened the crown feathers. The whole act lasted for only a split second and is therefore easily overlooked in nature. In a fourth case the dominant bird stretched one or both wings horizontally out and in again. In all four cases the dominant bird gained priority at the feeding table. Fluffing of body feathers may be exhibited both by dominant and subordinate birds.

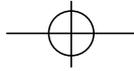
Extension of both wings shows three forms: (1) wings with spread primaries hanging down on each side of the body, (2) wings with spread primaries stretched more or less horizontally out from the body, (3) wings stretched out from the body with the primaries still kept tight together. Type 2 may be associated with fanned tail and open bill and may develop into an attack with physical combat.

Discussion

Agonistic encounters between several willow tits are nearly always accompanied by much vocalisation. In

the cacophony of sounds it is difficult, or even impossible, to assign the different calls to specific individuals. The most common sounds are gargles, *tää* calls, *zizi* and *spitt* alarm calls, *pjä* and staccato calls. All these ut-

Figure 5. Relationship between the number of gargles and intensity of aggression in willow tits. Numbers above columns denote number of encounters; vertical lines show 1 s.e. Aggression classes: (1) Opponents 'evaluating' each other, no attack; (2) light aggression, no attack; (3) light pursuit, light supplanting attacks (sensu Hinde 1952), no combat; (4) light clash; (5) clear aggression with attack, no combat; (6) attack with intense pursuit and combat.



terings appear to communicate aggression, alertness or excitement (Haftorn 1993), although much work remains to be done in order to clarify the multitude of possible information embedded in the willow tit's complex repertoire, including great variations of each main call. The *tää* note in the common call *si-tää*, for example, may vary from a single prolonged *täää* to a rapid series of extra short *tääs*, and it seems unlikely that such widely different types of the *si-tää* call convey the same message. Because the number of gargles increased significantly with the severity of aggression and culminated during encounters with physical combat (Fig. 5), gargle calls probably signify motivation for attack. Also *zizi* alarm calls occurred most commonly during physical fighting.

The body ruffling display of the willow tit is similar to the equivalent display in the black-capped chickadee *Parus atricapillus* and other species in the genus (Piaskowski et al. 1991). Piaskowski and co-workers suggested that the display functions in maintaining individual distance and gaining access to food. The single wing-flick display was first described for the black-capped chickadee visiting feeders during winter (Smith 1996). The display was most frequently elicited when a chickadee approached or remained close to another much higher-ranked individual. Smith had the impression that the displayer succeeded in obtaining food before retreating. None of the 11 displayers recorded by her was attacked by its opponent. In contrast, the wing-flicking willow tits observed by me were clearly dominants and the outcome of the contest in all three cases was that the subordinate bird stepped aside.

The function of the encounters described above is evidently manifold, with territorial claims and food competition being prominent causes. (1) When two neighbouring flocks meet, either at the territory border or inside one of the two territories, agonistic encounters seem inevitable. (2) The meeting of two flocks at a feeding table often leads to aggression. Other encounters may be associated with (3) establishment of social hier-

archies and (4) pair formation. There is growing evidence that juveniles usually pair in July–August, most likely before formation of winter flocks (Haftorn 1997). Further study is obviously needed to clarify fully the function of agonistic encounters in the willow tit and its relatives.

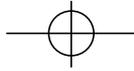
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A case of parental infanticide in the black stork *Ciconia nigra*

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Key words: infanticide, black stork, *Ciconia nigra*, brood reduction.

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Killing conspecific nestlings by an adult bird is usually observed in the context of sexually selected infanticide and it is the new breeding partner who kills the young (Hrdy 1979, Fujioka 1986, Banbura & Zielinski 1995). Very rarely chicks are killed by the parents (parental infanticide). Parental infanticide may save energetic resources otherwise wasted by a low quality chick that will probably not survive, and the resources saved may enhance the probability of successful fledging by the surviving brood members (Mock & Parker 1995).

However, parental infanticidal behaviour has been observed, for example, in the white spoonbill *Platalea leucordia* (Aguilera 1990), Heerman's gull *Larus heermanni* (Urrutia & Drummond 1990) and the white stork *Ciconia ciconia* (Schüz 1957, Jakubiec 1991, Tortosa & Redondo 1992, see also review by Mock & Parker 1997). This study reports a clear case of parental infanticide by the black stork *Ciconia nigra*.

The black stork is a rare species inhabiting Europe and Asia. In Poland the black stork occurs throughout the country with an estimated 950–1100 breeding pairs (Profus 1994). Black storks breed as single pairs in old, undisturbed forest areas, interspersed with streams, pools or swamps, where they feed mainly on small fish and amphibians. Black storks usually lay clutches of 3–4 (range 2–6) eggs and raise one clutch in the breeding season. Eggs are laid at 2-day intervals and incubation starts with the first or the second egg. Hatching is asynchronous and chicks fledge at age of 63–80 days (Cramp 1977, Keller & Profus 1992, Zawadzka et al. 1990).

Our observations were carried out on 11 and 18 June and 20 July 1978 in the Lochowskie Forest, about 70 km from Warsaw, eastern Poland. The black stork nest was situated about 10 m above the ground on an alder tree *Alnus glutinosa* in an alder thicket forest. The hide for taking photographs and observing storks was built gradually, about 13 m apart from the nest, starting with just a few branches, to accustom storks to the hide.

During the visit on 11 June an adult black stork was observed brooding five small chicks. On 18 June the nest was observed from the hide from 08.00 h to 14.00 h. There were still five chicks in the nest. All five chicks are clearly visible in Figure 2 (it is easiest to count bills) and Figure 3 (where one chick is seen falling). On that day, after arriving at the nest at about 09.00 h, a parent bird regurgitated a bolus of food consisting of many small items into the middle of the nest. The five chicks quickly swallowed all the regurgitated food from the nest bottom. No aggression was observed between the siblings. After feeding the parent stork rested at the edge of the nest for about 30 min. At 09.30 h the smallest chick was attacked for the first time during our observations. The parent bird (sex unknown) squeezed the head of the chick with the bill but let it free after a moment and flew away. The storks paid no attention to the observer hidden inside the hide as they already got used to it.

At 12.40 h the chicks were fed for the second time. A parent stork (sex unknown) returned with food and regurgitated it on to the floor of the nest. All five chicks quickly consumed the food. As before, no aggression among siblings was observed, nor did the chicks try to

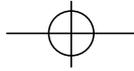


Figure 1. Black stork chicks feeding on regurgitated food. Photo by Grzegorz and Tomasz Klosowski.

insert their bills into the parent's mouth or grab the parent's bill. After feeding the parent stork was resting on the nest rim. At 13.00 h the parent bird seized the head of the smallest chick with the bill (Fig. 2) and threw the chick, which was still alive, out of the nest (Figs 3 and 4). The parent stork did not peck, shake or try to cannibalise the victim. The chick was killed by the fall to the ground. There were still some small fish in the throat of the dead chick lying under the nest, proving that it managed to take some food during the last feeding even though it was smaller than its nestmates.

The victimised chick was the smallest and the weakest of the brood. The difference in size and vigour was obvious when the chicks were observed from the hide. It can also be seen in Figure 2 that the victim had a smaller bill than the other chicks. In addition the primaries of the killed chick (Fig. 4) are hardly visible, while the

primaries and even secondaries of its nestmates are better developed and are clearly visible (Figs 1 and 2). The nest was visited again on 20 July and the remaining four chicks were seen standing on the nest ready to fly. All four chicks eventually fledged successfully from this nest in the second half of July.

It cannot be excluded that the killer was an intruding non-parental stork. However, the adult stork that victimised the chick first fed the nestlings, then rested for 20 min on the nest rim before killing the smallest chick. In addition, no aggression directed towards other nestlings was observed. Moreover, nests of black storks are isolated from each other by large distances. In the neighbouring Kampinoski National Park the average inter-nest distance was 3850 m (Zawadzka et al. 1990). It seems extremely unlikely that the killer was a non-parental bird.

In the nest observed here both the number of hatchlings (5 chicks) and the number of fledglings (4 chicks) were higher than average for lowland Poland. In the neighbouring Kampinoski National Park the average number of hatchlings per breeding pair was 3.53 ($n = 30$ broods) and the average number of fledglings per breeding pair was 2.69 ($n = 49$ broods) (Zawadzka et al. 1990). Thus, the infanticidal pair was caring for a large brood that was more costly to raise.

The chick that was killed was the smallest of the brood. In the white stork victimised nestlings were also the smallest in their brood and infanticidal pairs had broods larger than those of non-infanticidal storks (Tortosa & Redondo 1992). The parent black stork did not even try to eat the victim as has been observed in white storks (Schüz 1957, Tortosa & Redondo 1992), so the food advantage of cannibalism cannot explain infanticidal behaviour in the pair observed.

In most birds brood size is reduced through selective starvation of the weakest nestling, and the initial size hierarchy amongst chicks due to asynchronous hatching facilitates chick elimination in poor feeding conditions (Mock & Parker 1997). However, the indirect feeding method used by parent black storks, i.e. regurgitating large amount of small prey items on the nest floor, where it is accessible to all the nestlings (Cramp 1977), makes it impossible for siblings to monopolise the prey and also precludes parental control of food allocation amongst the chicks. In accordance with the prey-size hypothesis (Mock 1985) nestling aggression is low at this stage. Instead of fighting over food they

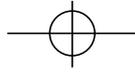


Figure 2 and 3. Twenty minutes later – the moment of infanticide. The parent black stork is ejecting the smallest chick from the nest. Photos by Grzegorz and Tomasz Klosowski.

cannot monopolise, chicks simply eat as fast as possible. As a result, even the least valuable offspring is able to feed for many days. Tortosa and Redondo (1992) advocate the hypothesis that if nestlings do not compete aggressively for food, parents should be selected to eliminate the extra chick themselves. The observed infanticidal behaviour in the black stork fits this view.

According to Simmons (1998), even in the absence of food stress selection for high-quality, competitive offspring is likely to overshadow selection for large number of young. The successful nestling may fledge at a heavier weight and dominate any surviving siblings, thus enhancing its present and future dominant position. Although comparative data concerning black storks fledging mass and subsequent survival are not available, in a similar species, the white stork, it was found that fledging mass decreases with increasing

brood size (Tortosa & Redondo 1992, Sasvári et al. 1999a). Thus, parental infanticide could also evolve as the product of selection for high offspring quality.

The recorded frequency of parental infanticide in the white stork is very low. Tortosa and Redondo (1992) witnessed only nine cases of infanticide out of 51 nests observed in Spain. In Hungary parental infanticide in the white stork breeding at both low and high density was not observed in any of 232 nests studied during a three year study (Sasvári et al. 1999b).

Unlike the well-studied white stork (Schüz 1957, Tortosa & Redondo 1992) direct killing of offspring by parents has never been observed in the black stork (Cramp 1977, Hancock et al. 1992). This may be due to very low frequency of parental infanticide, inadequate attention paid to this behaviour in the black stork, or both. Because black storks breed solitarily and usually

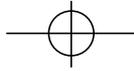


Figure 4. The victimised black stork chick under the nest. Photo by Grzegorz and Tomasz Klosowski.

in dense forests, it is very difficult to observe many nests of this species continuously. The frequency of parental infanticide in the black stork may well have been underestimated.

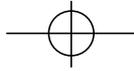
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Loss of song variation through cultural drift in nuthatches *Sitta europaea*: testing an hypothesis

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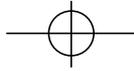
Nuthatches *Sitta europaea* have a relatively simple song with a small number of highly distinctive song types that are shared by most individuals in a population. In a previous study we showed that one song type (Ud) is lacking entirely from a large area in northern Belgium, and proposed the hypothesis that this song type has been lost through cultural drift in the previous century when the species' distribution was more fragmentary. We tested this hypothesis by collecting data on song types used by individual males in different regions and with a varying number of neighbours (zero, one or two), as well as playback experiments. We found a high frequency of song type matching in response to playback, supporting our basic assumption that birds adjust their songs to those used by neighbours. Preliminary observations suggest that song matching is also common among established neighbours and not just to intruders. Repertoire size of individual males increased with the number of neighbours, supporting the idea that founder effects may lead to loss of song types during colonisation. We examined the occurrence of song types in three populations with a known colonisation history and, as expected, found reduced song type diversity in the most recently founded population. However, since this was due to the absence of the same song type Ud that was found lacking in the population studied earlier, we cannot rule out the possibility that the two populations share a common ancestry. We conclude that our data support the proposed relationship between song diversity and isolation at the level of individual territories, which has rarely been shown in species with limited song type diversity. However, we need more evidence to rule out alternative explanations besides founder effects for the particular distribution of song types observed at a larger scale.

key words: Song, geographical variation, learning, playback, nuthatch.

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Bird song is remarkable among animal communication systems not only because of its high degree of variability within and among individuals, but also because it has been shown to be transmitted culturally (Catchpole & Slater 1995, Kroodsmas & Miller 1982). While this kind of transmission is fundamentally different from genetic transmission by inheritance, both processes are subject to similar evolutionary forces including copying errors (mutation), selection and drift (Burnell 1998, Catchpole & Slater 1995, Grant & Grant 1996, Nelson & Marler 1994). So far, these evolutionary forces have

been studied mainly in bird species with a large song variability at the population level, where few or no individuals sing the entire repertoire of song types or song variants present at the local level. In many of these cases, birds share more song types with their neighbours than with distant individuals, leading to neighbourhood groups of males with shared song types (e.g. Beecher et al. 1994, 2000, Bell et al. 1998, Catchpole & Rowell 1993, Lloyd et al. 1999, Molles & Vehrencamp 1999). At the individual level, males raised in isolation have been shown to develop smaller reper-



toires (Marler & Sherman 1985). Apart from this isolation-by-distance effect, several studies have also shown effects of physical isolation: small and isolated populations often show reduced song variation or complexity which has been attributed to founder effects and cultural drift (Baker 1996, Hamao & Ueda 2000, Thielcke & Wüstenberg 1985). In addition, drift may cause increasing differences among populations isolated from one another (Cicero & Benowitz-Fredericks 2000, Harbison et al. 1999).

Here we focus on spatial variation in the use of song types in a species with limited song variability, the nuthatch *Sitta europaea*. This species has a small number of simple, clearly distinctive song types which are used by the majority of individuals in a given population. The same five basic song types have been described from populations as far apart as Belgium and southern Germany (Löhrl 1958, Matthysen 1998). In a previous study we showed that one of these five basic song types ('Up-down' or Ud) is not present in a fairly large region (possibly several thousand km²) in the north of Belgium, while the same song type is heard frequently (between 10 and 20 % of all songs heard) in populations only a few tens of kilometers further south (Matthysen 1997). We hypothesised that this song type had been lost through cultural drift in the past, when the nuthatch population in this region was much smaller and perhaps limited to a small area near the city of Antwerp. When the population increased in the course of the 20th century – coincident with local increases elsewhere in western Europe (Matthysen 1998) – the missing song type would not have been able to reinvade this population because immigrants had no tutors from whom to learn the song type, or, if they had learned it previously, would tend to drop it from the repertoire by lack of response from neighbours (DeWolfe et al. 1989, Nelson 2000, Nelson & Marler 1994, Nordby et al. 1999). Thus, selective learning and/or attrition would act as barriers to cultural transmission of the lost songtype.

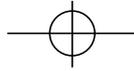
In this paper we provide further support for our hypothesis by testing two critical assumptions and one prediction. First, we tested the assumption that males adjust their usage of song types to that of their neighbours (song matching). This provides a straightforward mechanism for selective learning and/or attrition of songs in response to the neighbours' repertoires (Nelson 2000). Second, we tested the assumption that isolation leads to the loss of song types, by comparing re-

pertoire sizes between individuals with different numbers of neighbours, and this in three separate regions. Third, we predicted that mean repertoire size would be lower in more recently colonised nuthatch populations, due to founder effects. We therefore scored the presence of song types in three areas known to have been colonised by nuthatches during the 20th century. The history of expansion in Belgium and the Netherlands is relatively well documented (Matthysen 1998).

Study areas and methods

Observations were collected by two different observers in different years and study areas but with the same basic methodology. We first describe some of the aspects common to all observations. Study sites were selected based on habitat maps and previous knowledge of the regional occurrence of nuthatch populations. Study sites were either patches of mature broadleaved forest (mainly dominated by oak *Quercus robur*) or park areas with a more varied tree composition but also often dominated by oak, beech *Fagus sylvatica* and other large broadleaved trees. During preparatory visits, singing males were identified and approximate territory locations mapped. This was possible without marking individual males, because nuthatches have conspicuous territorial behaviour with loud vocalisations (Matthysen 1998) and because all observations were collected in fragmented forests or parks where patches of suitable habitat typically contained one or a few territories only. For the sake of data analysis, we identified clusters of neighbours among the studied territories where each cluster member's territory was within hearing distance of at least one other member. Observations were collected from 15 February to 14 April 1999 and from 19 March to 25 April 2001. Most observations were made between 07:00 h and 15:00 h. The order of visits was randomised as much as possible within observation days.

Nuthatch songs have a simple structure and can be easily assigned to the five basic song types without recording and spectrographic analysis. All songs are stereotyped repetitions of identical notes, characterised by a downward, upward or up-and-down inflection within the note. Based on note type and the number of notes per second, five song types have previously been defined: 'slow ascending' (Sa), 'fast ascending' (Fa),



'descending' (De), 'trill' (Tr) and 'up-down' (Ud) (Matthysen 1997, Matthysen 1998). Even though variation among males singing the same song type has not been studied, the basic song types are clearly recognisable in different males, even in different populations within Belgium and Germany (pers. obs.; Matthysen 1998).

In 1999 observations were collected by YD in ten sites to the south of Antwerp, within the larger study area described in more detail in Matthysen (1999). This area was chosen because it was known to represent the transition between populations with and without the song type Ud (Matthysen 1997 & unpublished data). Six of these sites contained only one singing male, the remainder had two ($n = 2$), three ($n = 1$) or four ($n = 1$) singing males. Most males were visited 13 to 17 times (one 19 times), but two males that disappeared during the study were visited only 8 and 9 times, respectively. During each visit we noted all vocalisations heard during the first 10 minutes, or if no song was heard, during a maximum of 20 minutes. Song-bouts were identified as a succession of strophes (a sequence of identical notes with short pauses) of the same song type, either followed by a pause of at least one minute, or a different song type (mean = 2.4 song bouts per 10-minute observation). Each visit was followed by a playback experiment in which the bird was presented with one song type (or call). Repertoire size was determined as the total number of song types heard during the observation period and/or in response to playback. In four territories we heard a particular song type in response to playback but not as spontaneous song. In one case an additional song type (Tr) was heard outside the observation or playback periods, but this was not included in the estimate of repertoire size.

For the playback we used two different tape recordings of each of the five song types and also of the most

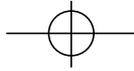
common call, the Excitement-Call (Matthysen 1998). Using two versions per song type was a compromise between the limited availability of good recordings (particularly for Ud) and practical considerations on one hand and, on the other hand, avoiding pseudoreplication (i.e. if variation in response is recording-specific, not song-specific). A short sequence of each vocalisation, obtained from commercial as well as personal recordings, was repeated several times to obtain a total time of 260 seconds, preceded by 10 seconds of silence. The playback (using a portable DEMCO DCR-101 cassette player) was started when the male was not vocalising, at a distance of 20 to 40 m from the male with a cassette player on the ground, and the observer at 20–30 m from the male and the playback source. The order of presenting song types (or call) to a particular male was chosen randomly and hence independent of previously heard vocalisations, while the two tapes per song type (or call) were alternated between playbacks of the same type to the same male. Most males reacted by rapidly approaching the playback source, sometimes climbing down to a few meters, and loud calling or singing. We noted the first vocalisation by the tested male as well as other vocalisations used for the duration of the playback. Song matching analyses were based on the first vocalisation only.

In the same year we also collected a limited number of observations on song sharing between two pairs of neighbours (in two different areas) that were frequently heard singing simultaneously. During four one- to two-hour observation periods per pair of neighbours, we noted all cases where a male started singing and the other male responded with song within 30 seconds. Song matching was defined as the proportion of these cases when the second male used the same song type as the first male.

In 2001 observations were collected by EH in three

Table 1. Characteristics of the study areas. Clusters refer to a set of nuthatch territories where each male was within hearing distance of at least one other male.

Name and approximate location	Year	Number of patches	Number of clusters	Number of males
Boom-Lier	1999	10	10	17
Zonhoven	2001	2	6	13
Vlaamse Ardennen	2001	4	5	13
Brugse	2001	3	5	9



regions where song had not been studied previously. The first region (Zonhoven) is in the centre of the Limburg province, for which the first breeding record dates from 1949. The population remained small and scattered (less than 100 pairs) until the late 1970s, but then started to increase to an estimated 800 pairs in 1992 for the entire province (see Matthysen 1998 for references). In this region nuthatches were located in patches of broadleaved forest inside a larger forest complex dominated by conifers (ca. 700 ha, 11 males), and also in one smaller area with oak forest (14 ha, 2 males). The second region (Vlaamse Ardennen) is a chain of forested hilltops dominated by oak and beech stands. Here the first breeding pairs were recorded in the 1960s, but again the main increase was in the late 1980s to over a hundred pairs at present (Matthysen 1998). In this area we located 13 territories in four forest patches from 3 to 40 ha. The third region consists of various forest patches and parks close to the city of Brugge, and was colonised as late as 1985 (Vlaamse Avifauna Commissie 1989). Here 9 territories were located in three different patches.

Because the purpose of the 2001 visits was to make a more rapid assessment of repertoire size of a larger number of individuals compared to the 1999 observations, we applied a different protocol. During the first four visits to each territory we noted all songs heard during 10-minute interval. Estimated repertoire size levelled off rapidly since in the fourth observation round new song types were heard in only 7 of 35 individuals. We then identified for each individual the song types that were not yet heard and played these back during one or at most two additional visits. We noted, over a maximum of 7 min, whether the previously unheard song type was used. All 'missing' song types (1 or 2, occasionally 3) were played back in succession during the same visit. The same playback tapes were used as in 1999. This protocol was based on the observation of a high degree of song matching in the 1999 observations (see Results). With this method we increased the estimated repertoire sizes of 16 males by, on average, 1.4 song types per male. Because the same protocol was applied in all areas and estimated repertoire size clearly approached an asymptote, we conclude that our observations gave a good estimate of differences in repertoire size among individuals and study areas.

Statistical analyses were performed in StatXact (Cytel Software Corporation 1995) for frequency data

(Fisher's exact test) and in SAS for continuous data (nonparametric correlation, generalised linear model using PROC GLM) (SAS Institute Inc. 1988).

Results

Geographic variation in song types

The five song types were heard in all study areas except Brugge, where Ud was never heard, neither spontaneously nor in response to playback ($n = 9$ males). Figure 1 shows the proportional use of the five song types in the four study areas. Overall, Sa was the most common song type and Tr and Ud the least common. Figure 2 combines the new data on the occurrence of Ud with results previously obtained by Matthysen (1997). Ud is frequently heard in populations in central Belgium, but less often in more distant study areas in different directions. The Boom-Lier population with 10 % Ud lies in a relatively sharp transition zone where the song type becomes rare or absent further north and east. Even within the Boom-Lier area, Ud was heard from all individuals in the most southwestern patch, but from only one in the other patches.

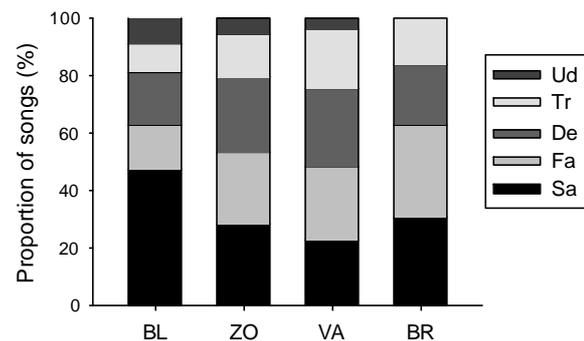


Figure 1. Proportional use of song types by nuthatches in the four study areas, based on all spontaneous song bouts heard during 10-minute observation periods (averaged over individuals per study area). Based on 8 to 19 visits per male in BL and four visits per male in the other areas; see Table 1 for numbers of males per area (BL = Boom-Lier, ZO = Zonhoven, VA = Vlaamse Ardennen, BR = Brugge).

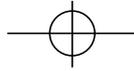
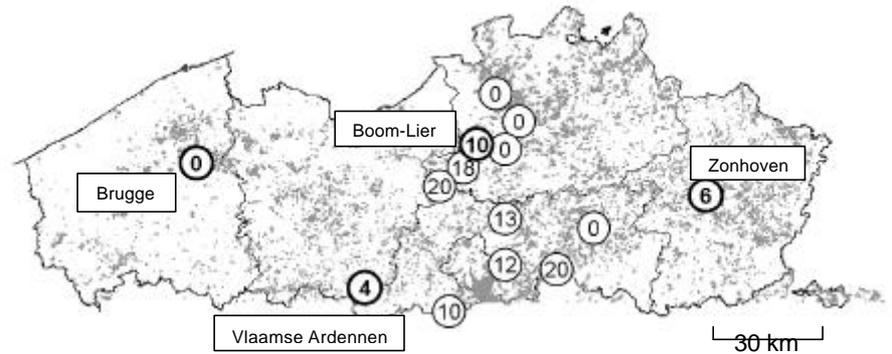


Figure 2. Proportional use of the nuthatch song type Ud (% of all songs heard) in different study areas, based on data in Matthysen (1997) and additional data presented in this paper (in bold). Shading indicates the distribution of forest.



Repertoire size

Repertoire sizes were analyzed separately for the two years of study, since they were obtained with different protocols. In the Boom-Lier area (1999 data) most individuals used four or five song types, but from two males we heard only three song types, and from one male only two. Overall, ten males never used song type Ud, one sang Ud but not De, one male did not sing Ud or Tr, and one lacked three song types, effectively singing only Sa and De. Mean repertoire size among clusters of neighbours (see Methods) increased significantly with the mean number of neighbours per cluster (Fig. 3: $r = 0.63$, one-tailed $P = 0.02$).

In the 2001 study areas, individual repertoire size varied between four and five in the Zonhoven and Vlaamse Ardennen areas (males differed only in the use of Ud), and between three and four in Brugge. In the latter area, no individuals sang Ud, and two individuals never used Tr either. Mean repertoire size was 3.8 in Brugge (the most recently colonised area), 4.7 in Vlaamse Ardennen and 4.2 in Zonhoven, the oldest population of the three. We tested the relationship between repertoire size and number of neighbours (Fig. 3) while taking into account the differences among study sites, using a generalised linear model. Repertoire size differed significantly between areas ($F_{2,12} = 7.5$, $P = 0.01$) and increased with the number of neighbours in a clus-

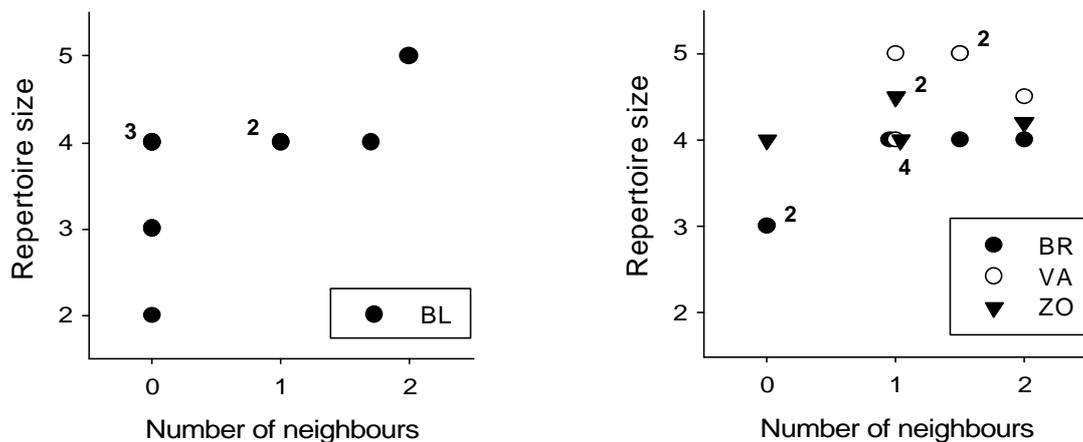


Figure 3. Relationship between mean repertoire size of nuthatches (total number of song types heard, spontaneously or in response to playback) and mean number of neighbours, using clusters of singing males as the unit of analysis. Data are shown separately for the four study areas visited in 1999 (left) and 2001 (right). Numbers indicate multiple data points with identical values. The increase in repertoire size with number of neighbours was statistically significant in both cases (see text).

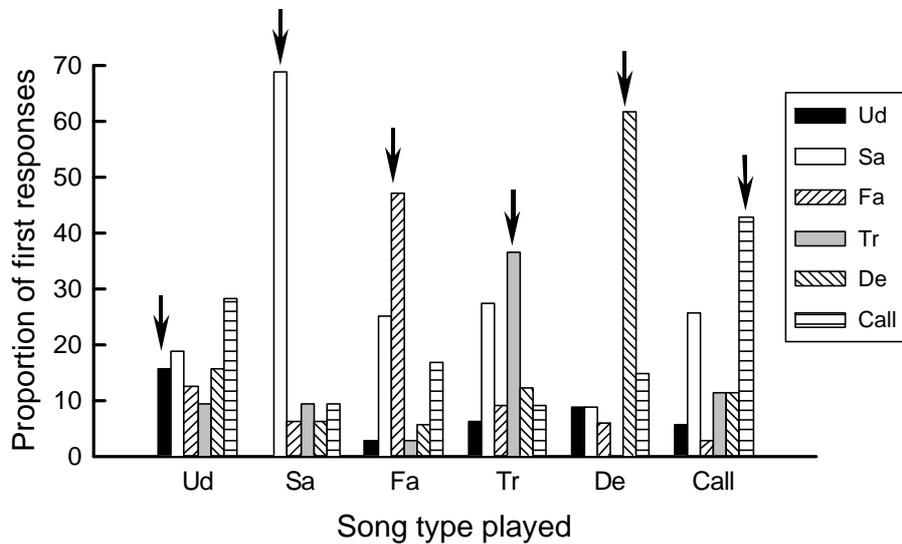
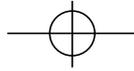


Figure 4. Responses of nuthatches to playback experiments with five different song types and the Excitement-call. Bars show the frequency of different vocalisations used as first response to the playback. Arrows indicate responses with the same vocalisation (total $n = 202$ positive responses out of 214 trials).

ter ($F_{1,12} = 6.2$, one-tailed $P = 0.015$) while the slope of this increase did not differ among areas ($F_{2,10} = 1.2$, $P = 0.4$) (Fig. 3).

Song matching

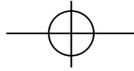
Nuthatches responded by vocalising in 94.4 % of the playback experiments (1999 data, $n = 214$ playbacks). In 46.0 % of all responses with vocalisation, the first heard vocalisation matched the playback ($n = 202$ playbacks). This exceeds by far the expected 16.7 % ($\chi^2_1 = 123$, $P < 0.001$) (if spontaneous song is independent of playback, matching is expected to occur in proportion

to each vocalisation's share in the playback, i.e. 1/6). Proportions of matching responses per male varied from 30 to 67 % with one exception (15.4 %). Figure 4 shows the frequency distribution of the vocalisation types as first response to playback of different song types and to the Excitement-call as well. Each vocalisation was answered most frequently with the same song type (or call), except for Ud where calling was the most frequent response, followed by Sa and then Ud (13 %). As a consequence, song matching frequencies were significantly heterogeneous among song types ($\chi^2_5 = 25.6$, $P < 0.001$; excluding Ud: $\chi^2_4 = 8.4$, $P = 0.08$). However, if only the five individuals were considered that were known to have Ud in their repertoire, Ud became the most common response with a frequency comparable to the other song types (46 %; see Table 2). All vocalisations were used in a much higher proportion in response to their own playback (3- to 5-fold) than to playback of other vocalisations (Table 2).

Observations on spontaneous song in two pairs of neighbours showed high rates of song matching (68 % and 84 %; $n = 88$ and 49; excluding calls). The matching rates were rather similar among song types (74 to 83 %) except for Ud (52 %, $n = 25$ observations in one neighbour pair only); however, the variation among the five song types was not significant (Fisher exact $P = 0.2$).

Table 2. Frequency of response (%) with different vocalisation types of nuthatches to playback of the same vocalisation or of other vocalisations, based on the first vocalisation used after playback. Each song type or call was played 1 to 4 times to 17 different males (total $n = 214$ playbacks).

	to same playback	to different playback
Ud	13.5	4.6
Sa	61.1	20.2
Fa	47.2	6.7
Tr	33.3	6.1
De	61.8	9.4
Call	42.9	14.5



Discussion

Our results support two basic assumptions underlying our hypothesis (Matthysen 1997) that song types have been lost through cultural drift in nuthatches. First, the playback experiment demonstrated a high degree of song matching: birds responded to about half of the playbacks by answering with the same song type (or call). This provides a situation in which song variety, or lack thereof, can be maintained even in the face of immigration, because immigrants receive strong reinforcement on the use of locally common song types, but not on foreign song types (DeWolfe et al. 1989, Nelson & Marler 1994, Nordby et al. 1999, Nelson 2000). Hence, immigration is not necessarily translated into 'meme flow' of song variants. Our preliminary observations on spontaneous song in two pairs of neighbours suggest that matching also occurs between established neighbours, and is not restricted to strangers as has been found in some studies (Falls 1985, Stoddard et al. 1992). A comparable degree of song matching towards playback was found previously in a German population (R. Schmidt, unpubl. thesis cited in Matthysen 1998) and in a previous study we have reported song matching in response to only one tested song type, Ud (Matthysen 1997).

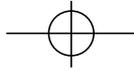
Second, we show that males with fewer neighbours tend to use fewer song types. We suggest that this reflects cultural drift on a small scale: isolated males have a higher chance of dropping a particular song from their repertoire, or not to acquire it when settling in the first place (cf. Marler & Sherman 1985). This explanation is supported by the observation that different song types can be absent in different males' repertoires, even though only one song type (Ud) was found missing on a larger (regional) scale. Apart from Ud, four males were not observed singing Tr, one lacked De, and one never sang Fa. It is interesting to note that apart from Ud, Tr is overall the least frequently used song type both in this study and the previous one (Matthysen 1997). Although chance events in cultural transmission can affect all variants in the 'meme' pool, it seems obvious that rarer variants (such as Tr in this case) are more prone to being lost. An alternative explanation for the observed relationship between repertoire size and number of neighbours could be that males without neighbours tend to live in the smallest habitat patches and might be of lower phenotypic quality (Møller

1991), which in turn may be expressed in a smaller repertoire size (Doutrelant et al. 2000a, Hasselquist et al. 1996, Møller et al. 2000). However, this seems unlikely because the forest patches we studied vary relatively little in size, and a previous study showed no relationships between patch size and either reproduction or survival (Matthysen 1999, Matthysen & Adriaensen 1998). Furthermore, this alternative explanation could not explain variation in repertoire size between populations.

Between-population differences in repertoire size or other measures of song complexity have been documented before (Peters et al. 2000 and references therein), particularly in the context of mainland-island comparisons (Baker 1996, Hamao & Ueda 2000). Still, most studies on geographic variation have focused on similarities and dissimilarities of song characteristics, rather than the amount of variation (Peters et al. 2000). Furthermore, the case of the nuthatch is unusual because the total number of song types is limited and the average male sings all available song types. As a consequence, variation is expressed only through some individuals or populations lacking particular song types. This contrasts with the more typical – or at least better-studied – situation in songbirds where an individual male sings only a fraction of the song variants present in the population (Beecher et al. 2000).

A crucial and unanswered question is when and how nuthatches acquire song. To date there have been no specific studies or experiments on this aspect. However, song is rarely heard during and particularly after the nestling period (Matthysen 1998) and its function in territorial defence in the non-breeding season is entirely taken over by calls. It is therefore likely that young males have limited exposure to the different song types before they disperse. Except for sporadic singing in September, song activity is resumed gradually from December when the main phase of dispersal and territory establishment is over (Matthysen 1998). Anecdotal observations on males with imperfect song in late winter (Matthysen, unpubl.) support the idea that song is not yet fully developed after settling, and experience with neighbour song can have a significant influence on both song performance and the repertoire. However, this hypothesis needs formal testing.

In addition to previous work this study provided further information on the geographical distribution of song types in northern Belgium. We found another po-



pulation lacking the Ud song type, corresponding to the most recently colonised area so far studied (Brugge). The late colonisation of this region is probably explained by its relative isolation from other forest-rich areas (see Fig. 2). In the two remaining populations, both of them colonised over 40 years ago, all song types are represented. This confirms our prediction that more recently colonised populations should be more likely to lack certain song types, because an initial founder effect would have been less likely to be counteracted by cultural diffusion. Nevertheless, the geographical pattern remains open to alternative explanations, because Ud is still the only song type that we found lacking from larger areas. Furthermore, even where Ud is present, its frequency is highly variable between populations, varying from 4 and 6 % in Vlaamse Ardennen and Zonhoven (this study) to 20 % in some previously studied populations (Matthysen 1997). There are several possible explanations for this particular pattern besides, or in addition to, cultural drift. First, different populations may not be independent of one another. For instance, the Brugge and Zonhoven populations might have been colonised by birds originating from the Antwerp region that did not sing Ud. Second, Ud may be more difficult to learn and/or to maintain for birds not exposed to it, perhaps because it is intermediate in note structure between the common song types Sa and De (Löhrl 1958, Matthysen 1998). Song matching rates to Ud appeared to be the lowest of all song types, both in the playback experiment and the spontaneous observations. However, these observations were based on a small number of Ud singers and require confirmation. A third possibility is that there is an unknown selective factor acting against Ud in the northern parts of Belgium. Two possible factors are differences in the acoustic environment (Brown & Handford 2000, Morton 1975) and song divergence in the presence of a related species (Doutrelant et al. 2000b). Since nuthatches occupy very similar habitats in all studied populations and have no close relatives or direct competitors with a similar song, this hypothesis appears unlikely.

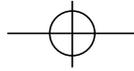
We conclude that, even though our study supports the hypothesis that isolated nuthatch populations can lose song types through cultural drift, we need additional evidence to show that this hypothesis also explains the particular distribution of song types. We suggest that future research should investigate the distribution of song types on an even larger scale, as well as the mechanisms

of song acquisition and transmission in nuthatches and other species with limited song type diversity.

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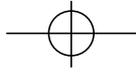
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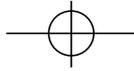


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Gust soaring as a basis for the flight of petrels and albatrosses (Procellariiformes)

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The classical theory of wind-gradient soaring requires an albatross to climb against the wind without losing air speed, relying on the increase in the wind strength as it climbs to offset the deceleration due to the climb. A simple calculation shows that a strong enough wind gradient could only be expected up to a height of about 3 m above the surface, in conditions where albatrosses typically pull up to around 15 m. Rather than extracting energy continuously from the wind gradient in a sustained climb, it is more effective to obtain pulses of energy at low level, by flying through regions of separated flow behind wave crests, out into the unobstructed wind. Much more energy is extracted by receiving such a gust from the ventral side than from ahead. The typical behaviour of albatrosses is to roll belly-to-wind to a very steep angle of bank, as they pull up out of a separation bubble, when crossing a wave crest to windward. This manoeuvre delivers a pulse of kinetic energy corresponding to an 'energy height', which is sufficient to account for the observed height of pullups. These were highest when stepping from wave to wave, down-swell. Alternatively, the energy can be used to penetrate into wind, close to the surface. Less energy height is available to smaller species from a gust of given strength, and their observed pullups were not so high as those of albatrosses.

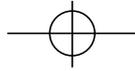
Manoeuvring in response to gusts would require fast and accurate monitoring of very small dynamic pressures, of the order of a few millimetres of water, calling for a sense organ more sensitive than any existing aircraft air speed indicator. It is suggested that the forward-pointing tubular nostrils of Procellariiformes ('Tubinares') serve as pitot tubes, and that the large nasal sense organ is (at least in part) an organ that monitors dynamic pressure. The implication is that only tube-nosed birds have the sensory ability to take advantage of the energy in gusts due to flow separation over wave crests. This is an unlimited source of energy, available in abundance wherever winds of medium speed create the right surface conditions. Gannets and boobies do not have tubular nostrils, although they are otherwise quite similar morphologically to small albatrosses. Their flight is entirely different, relying heavily on flapping, with only a limited capacity for slope soaring along ocean swells (swell soaring). Their distribution is very restricted in comparison to that of petrels and albatrosses, which can roam freely anywhere over the oceans.

Key words: albatross, flight, soaring, ocean.

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The petrels and albatrosses (Procellariiformes) are the dominant flying birds of the open oceans, especially in the windy middle latitudes of the southern hemisphere.

They comprise nearly 100 species, some of which are very abundant, ranging in mass from about 20 g for the smallest storm-petrels to over 9 kg for the largest



albatrosses. It is generally believed that their success is connected with a method of soaring, whereby they somehow extract energy from the horizontal motion of the wind relative to the water surface. I propose that they do this by extracting pulses of kinetic energy from discontinuities in the wind flow ('gusts'), rather than by exploiting a continuous wind gradient as previous authors have argued, and that their soaring technique depends on an air speed sense mediated by the characteristic tubular nostrils, from which the group derives its alternative name 'Tubinares'. Marine birds of other orders, such as the Pelecaniformes and Charadriiformes show neither the tubular nostrils nor the associated flight behaviour. They are less widespread, and appear to be restricted to smaller foraging radii when nesting.

Wind gradient soaring – the classical theory

Tickell (2000) exhaustively reviewed theories about albatross flight, which are all variations on the classical theory that gliding flight could be sustained by a gradient in the horizontal wind, increasing in strength with height (Rayleigh 1883). Starting at the surface, the theoretical albatross heads directly into wind and angles its flight path upwards. As it climbs, it slows down, relative to the sea, but if the wind speed increases strongly enough with height to compensate for this, its air speed is maintained, or increases. It gains height without losing air speed, even though the air is not rising. Likewise, the albatross could gain additional air speed by descending through the wind gradient on a downwind heading. No glider pilot has yet claimed to have used this method for sustained soaring, but all pilots are familiar with the converse effect, whereby descending through a wind gradient, when heading into the wind for landing, can cause a potentially dangerous *loss* of air speed.

There is a compelling elegance about the concept of an albatross rhythmically climbing and descending through a mathematically definable wind gradient, which was irresistible to physicists in the nineteenth century, and retained its appeal throughout the twentieth. Idrac (1924) was the first to undertake scientific studies of albatross flight at sea, and his interpretation was echoed by Admiral Jameson's (1958) eye-witness descriptions from the bridge of an aircraft carrier. Cone (1964) based a mathematical theory on Jameson's account, and this in turn became the basis of the compu-

ter simulations of Wood (1973) and Sachs (1993). These all represent essentially the same theory of 'dynamic soaring' in which the increase of wind speed with height is the source of the energy that keeps the bird flying. However, there are some problems in reconciling this idea with field observations, one of which is that albatrosses pull up far above the height at which the wind gradient could be expected to be strong enough to maintain air speed in the climb.

Required wind gradient for sustained climb

How strong would the wind gradient need to be? Figure 1 shows a (dragless) albatross of mass m (weight mg) gliding at an air speed V on a flight path that is inclined upwards, at an angle α above the horizontal. The component of its weight in the direction opposite to the flight path is $mg \sin \alpha$, which causes the albatross to decelerate at a rate $g \sin \alpha$, where g is the acceleration due to gravity. On the other hand, if the wind speed (V_w) is an increasing function of height (h) above the surface, then the slope of this function (dV_w/dh), times the vertical component of the bird's air speed ($V \sin \alpha$), gives the rate of increase of air speed due to the wind gradient. This must equal or exceed $g \sin \alpha$, if air speed is to be maintained:

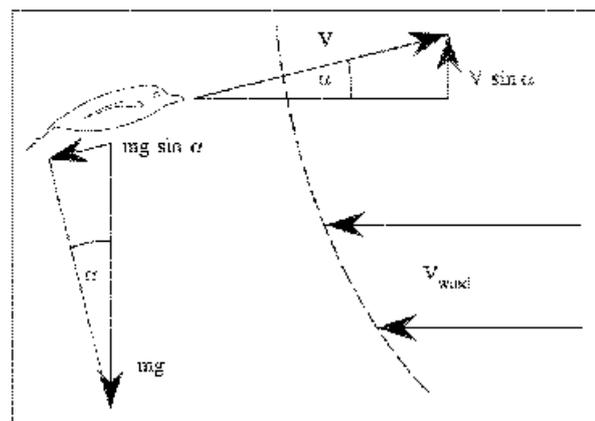
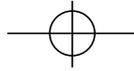


Figure 1. An albatross gliding 'uphill' slows down because a component of its weight is directed backwards along the flight path, but if it heads into wind, it also climbs through layers of increasing head wind. Air speed is maintained in the climb if the rate of increase of air speed, due to increasing wind, equals or exceeds the deceleration due to gravity.



$$g \sin \alpha \leq (V \sin \alpha) (dV_w/dh). \quad (1)$$

The value of the wind gradient just sufficient to maintain air speed is therefore

$$dV_w/dh = g/V, \quad (2)$$

regardless of the angle of climb. An albatross flying at an air speed of 20 m s^{-1} , with gravity around 10 m s^{-2} , could maintain air speed in a wind gradient of around 0.5 s^{-1} , meaning that the wind speed increases by 0.5 m s^{-1} , per metre of height. This calculation is based on optimistic assumptions. If the albatross were not dragless, or flew slower than 20 m s^{-1} (rather fast for a gliding albatross), then the wind gradient would have to be stronger.

How strong is the wind gradient likely to be? That question is traditionally answered in terms of a simplified ocean, whose surface is flat, so that the height (h) can be unambiguously defined. For problems where such an approximation is acceptable, a logarithmic function is commonly used (Sutton 1953):

$$V_w = V_{wa} [\ln(h/h_r) / \ln(h_a/h_r)]. \quad (3)$$

V_{wa} is the reading of the anemometer, which is set at a height h_a , while V_w is the estimated wind speed at some other height h . The shape of the wind profile is adjusted by the 'roughness height' h_r , for which a medium value is 10^{-3} m. Differentiating equation (3) with respect to h yields a hyperbolic shape for the wind gradient:

$$dV_w/dh = V_{wa} / (h \ln(h_a/h_r)). \quad (4)$$

The wind gradient is theoretically infinite at the surface, and decreases with height, until it eventually becomes imperceptible, i.e. any further increase of wind strength with height is masked by random fluctuations. Pennycuik (1982) made the rough-and-ready observation that on a day in the South Atlantic when the wind was about 15 m s^{-1} , as measured by a masthead anemometer at a nominal height of 25 m, wandering albatrosses *Diomedea exulans* and black-browed albatrosses *D. melanophris* were pulling up to around 15 m, as judged against the horizon from various decks on the ship. According to equation (4), the wind gradient at that height would be about $1.5/h$, that is 0.1 s^{-1} at 15 m. This is not nearly enough to sustain even a dragless al-

batross pulling up at an unusually high speed. Although equation (3) is approximate at best, the wind gradient would have to be almost linear to reach 0.5 s^{-1} at 15 m, and that is even less realistic. The optimistic assumptions above would have allowed the albatrosses to pull up to about 3 m, which is only about one wing span in the case of a wandering albatross. It is not likely that the albatrosses would have been able to build up speed near the surface in order to continue the climb above the level of the critical wind gradient because, as soon as the speed starts to drop, the reduced speed itself raises the strength of the wind gradient required (equation 2). This regenerative effect would terminate the climb abruptly. Wilson (1975) suggested that an albatross might build up speed by soaring along the windward face of a wave, and then pull up by converting excess kinetic energy into potential energy. The speed ranges observed in albatrosses flying over the sea did not exclude this, but their behaviour suggests a different explanation.

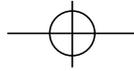
Field observations

Study area and period

The following remarks are based on video and visual observations of flight behaviour, collected at sea on the British Antarctic Survey's ship RRS *James Clark Ross* in January 1994, between latitudes 50° and 61° S and longitudes 35° and 59° W, spending the most time to the north of South Georgia. Wind speeds ranged from 3 to 24 m s^{-1} . Usable samples of observations were obtained on three albatross species, and three smaller species, which are listed in Table 1, together with measurements obtained on an earlier visit to Bird Island, South Georgia, and updated with additional measurements obtained in 1994.

Pullup behaviour

Albatrosses and medium-sized petrels pulled up frequently in winds of medium strength, but were never seen climbing steadily into wind with their wings level, as described by Jameson (1958). On the contrary, these pullups were characterised by extreme angles of bank, typically 60 – 70° (sometimes past the vertical) with the bird's ventral side facing the wind. In all cases the pull-

**Table 1.** Body masses and wing measurements. The three-letter codes identify the species in the figures.

Species		Code	Mass (kg)	Span (m)	Area (m ²)
<i>Diomedea exulans</i>	Wandering albatross	WAN	8.46	3.01	0.592
<i>Diomedea melanophris</i>	Black-browed albatross	BBA	3.08	2.19	0.354
<i>Diomedea chrysostoma</i>	Grey-headed albatross	GHA	3.68	2.18	0.334
<i>Procellaria aequinoctialis</i>	White-chinned petrel	WCP	1.08	1.41	0.167
<i>Pachyptila desolata</i>	Antarctic prion	PRN	0.155	0.635	0.0469
<i>Oceanites oceanicus</i>	Wilson's storm-petrel	WIL	0.0345	0.396	0.0216

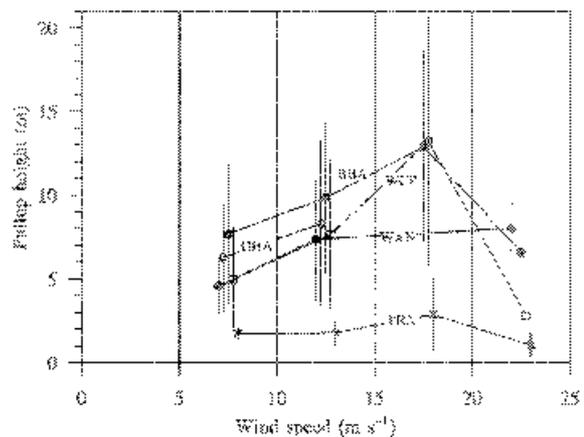
up was initiated as the albatross passed over the crest of a wave towards the windward slope, very close to the surface. At this point the albatross would roll belly-to-wind, at the same time angling the flight path steeply upwards. The subsequent sequence of manoeuvres, as well as the height of the pullups, varied depending on the bird's direction of travel relative to the swell.

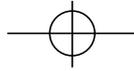
An albatross stepping from wave to wave in the direction in which the swell was moving ('down-swell') would level its wings at the top of the pullup, then glide downwind to another wave, before turning back into wind close to the surface, to initiate another pullup. These downwind glides through the wind gradient were the only manoeuvres that resembled any part of Jameson's (1958) description of the soaring cycle. An albatross travelling 'across-swell', i.e. doing repeated pullups along the same wave, would not level its wings at the top of the pullup, but would continue in a steeply banked arc, arriving back at the surface on an obliquely downwind heading. Before initiating another pullup, it would turn back to an obliquely windward heading, banking at a moderate angle (20–30°), and flying so low over the top of a wave that no space could usually be seen between the windward wing tip and the water surface, although the wing tip almost never actually touched the surface. This sequence of a pullup followed by a low, into-wind turn, was often regularly repeated, so that an albatross proceeding across-swell, viewed from a distance to windward, would present regular flashes of white as it pulled up and rolled its ventral side towards the observer.

Wandering and black-browed albatrosses were often able to catch up with, and overtake the ship when it was steaming directly into wind, flapping their wings infrequently or not at all. An albatross penetrating to wind-

ward would spend most of its time gliding into wind and up-swell, very close to the surface where the wind is minimal, and the drag of its wings is reduced by ground effect. When the glide could no longer be sustained, the albatross would pull up as it crossed the crest of a wave, turning right or left and rolling to present its ventral side to the wind. As it returned to the surface, it would turn back into wind, and initiate another long glide in ground effect.

In all of these cases, the albatross appears to replenish its reserve of kinetic energy whenever it pulls up and rolls its ventral side to the wind. This energy 'pulse' is then used to gain height in a high pullup if the albatross is travelling downwind, or alternatively it is expended more gradually against drag in a long, into-wind glide in ground effect.

**Figure 2.** Pullup height versus wind strength (means with standard deviation bars), in categories of 5 m s⁻¹. No observations were obtained in wind speeds below 5 m s⁻¹. Species codes are in Table 1.



Height of pullups

The 'height' of a bird above the surface of the ocean cannot be measured or defined in any exact way, because the surface is not flat, and its shape is constantly changing. However, some species pull up higher than others, and higher in some conditions than in others. Two methods were used to give a rough indication of these differences, although neither could be considered repeatable to the point where statistical analysis would be justified. First, the observer's eye height relative to a calm sea was known, when standing on various decks, and the height of a pullup could be judged by whether or not the bird appeared to cross the horizon. For lower pullups, the height could be judged in multiples of the bird's wing span, and later converted into metres, knowing the wing span of each species. Pullup heights, judged by one or other of these methods for five of the six species in Table 1, are shown in Figures 2 and 3.

Figure 2 shows pullup heights classified into broad categories of wind speed. Those species that pulled up above 10 m performed the highest pullups in wind speeds between 15 and 20 m s⁻¹. In Figure 3, pullup height is plotted against step direction relative to the swell. Pullup heights were least for birds stepping up-swell, and progressively higher in the across-swell and down-swell directions. The three albatross species (wandering, black-browed and grey-headed albatross *D. melanophris*) and the white-chinned petrel *Procellaria aequinoctialis* all showed much the same pattern in both graphs, as did the Antarctic prion (*Pachyptila desolata*), although its pullup heights were lower. Wilson's storm-petrel *Oceanites oceanicus* does not appear in Figures 2 and 3, because it was not seen pulling up at all.

Energy exchange

Kinetic energy height

A bird or aircraft travelling fast can convert excess kinetic energy into potential energy by pulling up, but this does not constitute soaring. The objective of any form of soaring is to maintain or increase height without a corresponding loss of speed, or alternatively to gain speed without losing height. The principle is that kinetic and potential energy are inter-convertible, and to-

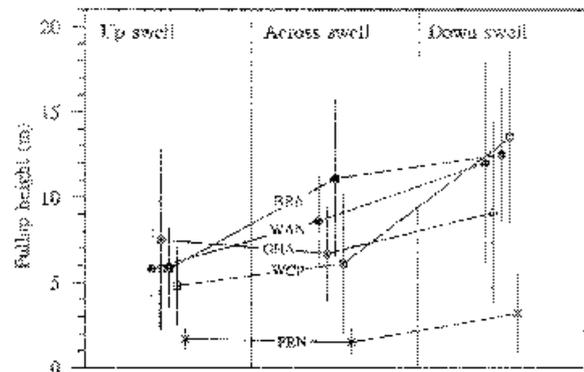


Figure 3. Pullup height versus step direction. Species codes are in Table 1.

gether constitute 'total energy', but this is valid only if kinetic energy is defined in one particular way. Kinetic energy (E_k) is:

$$E_k = mV^2/2, \quad (5)$$

where m is the bird's mass and V is its speed – but speed is relative, and equation (5) is meaningless until the frame of reference, against which the speed is to be measured, is specified. In principle, the choice is arbitrary, but only one choice has the property that kinetic energy is exchangeable with potential energy. For that, the frame of reference must be fixed to the air through which the bird is flying at the current moment. V must be defined as the bird's air speed, not the speed relative to the ground or the sea surface.

This may appear counter-intuitive, but it can be un-

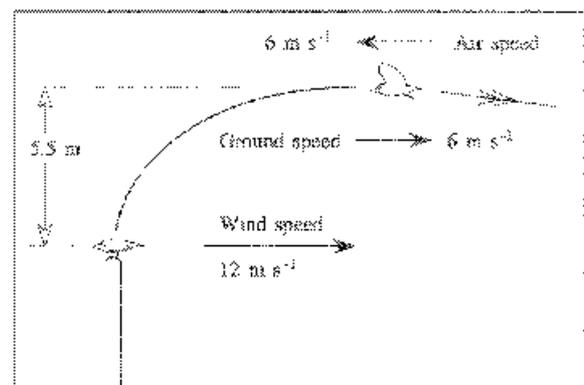
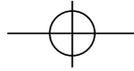


Figure 4. Gull converting kinetic energy into potential energy (see text).



derstood from Figure 4, which shows a gull standing on a post, with its wings folded. Its ground speed is zero, and its kinetic energy, if calculated from the ground speed, would also be zero. However, its air speed is 12 m s^{-1} , because that is the wind speed. Although the gull is stationary (relative to the ground), the kinetic energy based on its air speed is real, in the sense that the gull can immediately convert it into potential energy, simply by opening its wings. If it does that, it rises and slows down relative to the air, 'converting speed into height' as pilots say, until it is flying at its minimum air speed for gliding and cannot slow down any further. If its initial air speed was V_1 , then from equation (5), the amount of kinetic energy ΔE_k which it loses by slowing down to V_2 is

$$\Delta E_k = m(V_1^2 - V_2^2)/2. \quad (6)$$

To convert this loss of speed into a gain of height (h_k) the lost kinetic energy must be changed into an equal amount of potential energy:

$$m(V_1^2 - V_2^2)/2 = mgh_k, \quad (7)$$

where g is the acceleration due to gravity. The height gained is therefore

$$h_k = (V_1^2 - V_2^2)/2g. \quad (8)$$

This 'kinetic energy height' depends on the starting and finishing speeds, and on the strength of gravity, but not on the mass of the bird. The mass (m) cancels in equation (7). In practice, the bird will climb a little less than h_k , because some energy is lost in overcoming drag. If we set $g = 9.81 \text{ m s}^{-2}$, and assume that the gull's air speed slows down from 12 to 6 m s^{-1} , then $h_k = 5.5$ metres. At the top of the climb the gull is flying at 6 m s^{-1} against a head wind of 12 m s^{-1} , so that, relative to the ground, it is carried along backwards at 6 m s^{-1} . No further energy can be obtained, either from the wind or from the gull's own motion. It continues backwards at 6 m s^{-1} , sinking steadily earthwards (owing to drag) until it either arrives on the ground, or starts flapping.

Kinetic energy based on ground speed

To non-pilots it often appears more appropriate to define kinetic energy in terms of ground speed, but although

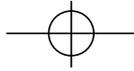
this is mathematically legitimate, the energy so defined has different properties. Looked at in this way, the gull begins with no kinetic energy when it is standing on the post, then its potential and kinetic energy both increase at the same time, as it climbs and accelerates backwards. As kinetic energy is *gained* in the climb, it clearly does not come from potential energy. It comes from the wind, and is the amount of energy that would be dissipated, should the gull be so unfortunate as to collide with a stationary object. This energy cannot be used by the gull to increase its height.

Cone (1964) committed no mathematical error in calculating an albatross's kinetic energy from its ground speed, but the choice was inappropriate to a discussion of soaring, because the energy so calculated is not convertible into potential energy. Cone reached the bizarre conclusion, repeated by Sachs (1993), that the most important gain in kinetic energy occurs as the bird turns downwind at the top of the climb, because it acquires a high ground speed, as it is swept away by the wind. Many an aviator's career has ended prematurely as a result of mistaking a high ground speed, when flying downwind, for usable 'flying speed'. The misunderstanding comes to light on attempting to turn into wind and land, often with fatal results. Air speed can be converted into height, or used for manoeuvring, but ground speed cannot. Kinetic energy based on ground speed exists, but is irrelevant to the albatross' objective, which is to keep flying without doing muscular work. The objective of dynamic soaring is to maintain or gain air speed, not ground speed.

Gust soaring

The boundary layer over the ocean

The classical theory of wind-gradient soaring departs from reality as soon as it postulates an albatross flying over a definable surface, with the wind speed increasing smoothly with height. These conditions do not exist over the ocean. The surface is never flat, nor does it undulate in simple mathematical patterns. Unlikely as it may seem, the layer of air that is actually in contact with the water surface has no motion relative to the water – the so-called 'no-slip condition' (Lighthill 1986). The 'boundary layer' is the zone of transition between this lowest layer, and the unobstructed wind up above. The



wind speed builds up through the boundary layer, but not in such a smooth and simple way as indicated by equation (3). To some degree the boundary layer undulates up and down, following the wave contours, but where a wave starts to curl over, the boundary layer cannot follow the sudden downward change of direction. It separates from the water surface at the wave crest, re-attaching in the trough. Below the separated boundary layer, in the lee of the crest, is a 'separation bubble' where the wind speed is light, and the direction is confused. Spray blown from the wave crests falls and loses its motion in the separation bubbles, and sailing boats lose the wind if the separation bubbles are large enough, as they may be in the long swells of the Southern Ocean.

Scorer's observation

Besides the albatrosses (Diomedidae), many species of petrels and shearwaters (Procellariidae) and storm-petrels (Hydrobatidae) skim over the crests of the waves, in and out of the troughs. As a bird passes in and out of the separation bubbles in the lee of wave crests, it encounters sudden shifts of wind speed and direction, both horizontal and vertical, which can be used to replenish its kinetic energy. It is not practicable to construct a mathematical model or computer simulation which explicitly represents this, but it is possible to observe the manoeuvres of different species in a more qualitative way, and interpret them from a glider pilot's point of view. Scorer's (1958) book about the aerodynamics of the atmosphere contains many acute observations about the flight of soaring birds, as seen by the eye of a glider pilot, including this one:

'Smaller ocean birds, and possibly albatrosses too, exploit the gradients of wind at the edges of the wakes at the wave crests. They are remarkable to watch because they often rise no more than 2 or 3 m above the sea surface for several minutes and yet are not seen to flap at all. They appear to behave roughly as follows: they pass up the lee side of a wave from the top of which the flow separates; as they traverse the edge of the wake they experience a sudden increase in air speed which they use to gain 2 or 3 m of height. During their ascent they choose their future path among the moving waves so as to avoid the wakes. While on this path they gradually lose air speed and when they are near to stalling they turn sideways into the wake of a wave. Here they receive momentum towards the wave from the air

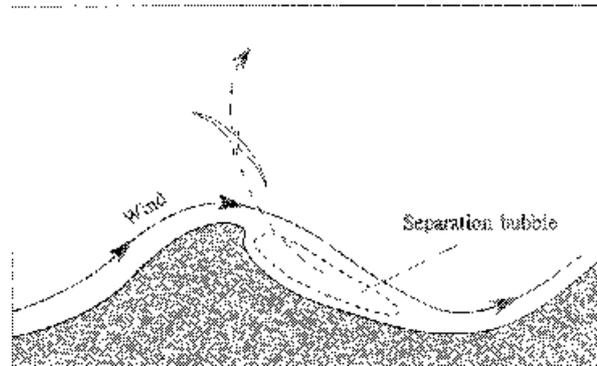


Figure 5. Scorer's (1958) concept in which a bird gains air speed by pulling up out of the separated wake behind a wave crest, into the unobstructed wind flow.

which is moving in the direction of the wind more slowly (if at all) than the air from which they have just come. They can then gain air speed by passing over the wave crest as before.'

By 'wakes' Scorer meant the separation bubbles on the downwind side of the wave crests, which form in wind speeds above about 5 m s^{-1} , as the wave crests begin to curl over (Fig. 5). A bird that pulls up out of a separation bubble is struck by a sudden blast of wind as it enters the unobstructed air flow above. Provided that the bird is favourably oriented, its air speed increases, and it gains a pulse of kinetic energy, that is convertible into potential energy. The bird gains energy from 'gusts', that is from discontinuities in the speed and direction of the wind. The technique of 'gust soaring' requires the bird to anticipate these discontinuities, and to choose its flight path so as to be favourably oriented as it flies through them.

Surge due to a sharp-edged gust

A 'gust' is understood in aeronautical engineering to mean a sudden change (predictable or not) in the relative speed and/or direction of the air flow, as a bird or aircraft passes from one region of air into another. The glider at the top of Figure 6 is flying steadily along, with its weight (mg) balanced by the aerodynamic reaction force on the wing (R). It is about to encounter a 'sharp-edged gust', a phenomenon which does not actually exist, but which is much used in aircraft design calculations. Seen from the pilot's viewpoint, the glider is

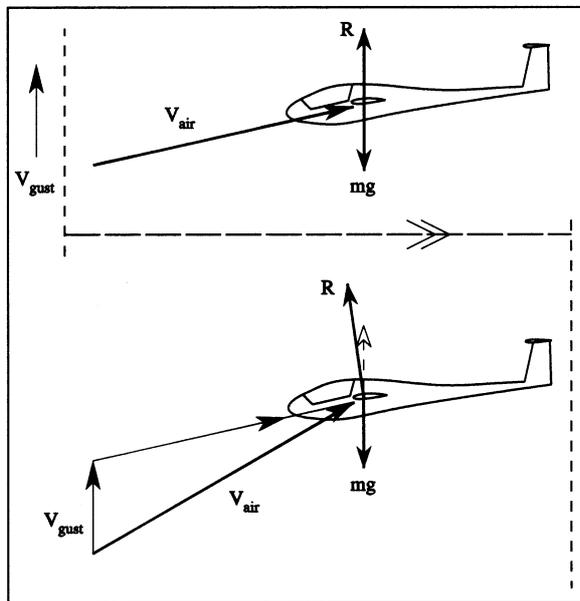
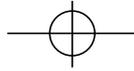


Figure 6. Glider entering a sharp-edged gust (see text).

sustained in equilibrium by a relative wind (V_{air}) which comes from ahead, and also from slightly below the horizon, because of the glider's sinking speed. This is the 'wind-tunnel' frame of reference, in which the glider is perceived as stationary, with the air moving past it. It is equivalent to regarding the glider as moving through stationary air, for effects that only involve the relative motion between the glider and the air, including gains of kinetic energy (above). Just ahead is a sharp boundary (vertical dashed line), beyond which the air is moving upwards at a speed V_{gust} , relative to the air in which the glider is currently flying. This boundary is coming towards the glider, and a moment later, it has swept past it (lower figure), giving the glider an additional vertical component of velocity, effectively increasing its sinking speed by an amount equal to V_{gust} . Adding this vectorially to the air speed that the glider already had, V_{air} is now larger than before, and also strikes the wing at a steeper angle, i.e. the angle of attack has increased. So long as the wing was not already near its stalling angle, the effect is that the total reaction force (R) increases, so that it now exceeds the weight, and also rotates, so that it is now inclined forwards.

Although it is a simplified scenario, Figure 6 resembles what happens when a glider flies with its wings level into the core of a thermal. The pilot experiences a

'surge', which is actually a combination of two effects, one immediate and one delayed, each increasing the glider's total energy (sum of kinetic and potential energy). First, there is an immediate increase in air speed, causing the air speed indicator needle to jump, and corresponding to an increase in the kinetic energy according to equation (6). Then the glider continues to accelerate upwards and forwards, because of the unbalanced component of the reaction force R . Assuming that the new air mass continues indefinitely with no further changes of speed, the glider eventually returns to equilibrium, having gained some height and/or some speed relative to the new air mass.

Energy gained from the gust

The stability of the glider, and the actions of the pilot, determine the proportions in which the energy gained is divided between kinetic and potential forms, but do not affect the total energy gained. We can imagine that the glider has an extremely fast autopilot, which holds the vertical component of R exactly equal to the weight, so that the glider accelerates forwards but not upwards. In that case, all of the delayed energy comes in the form of increased air speed, and the amount of the speed increase can be determined if we can estimate a polar curve for the glider. Figure 7 is a glide polar for a Wandering Albatross, computed for sea level from the data in Table 1, using the program FLIGHT.BAS from <http://detritus.inhs.uiuc.edu/wes/pennycuick.html>. The

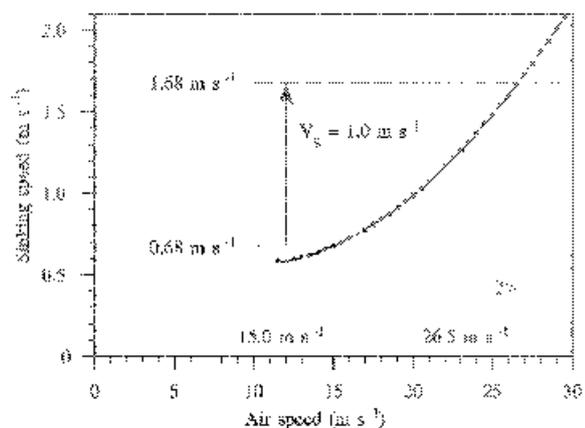
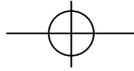


Figure 7. Computed points on a glide polar for a wandering albatross. A parabola, fitted through the points, has been used to find the kinetic energy gained from a gust of 1 m s^{-1} , striking the bird from its ventral side.



albatross is initially gliding at 15.0 m s^{-1} , which is near the mean speed at which this species was observed flying over the sea by Pennycuick (1982). According to the computed polar, the corresponding sinking speed is 0.68 m s^{-1} . The albatross now encounters a sharp-edged gust like the one in Figure 6, with a gust velocity of 1 m s^{-1} . Its sinking speed relative to the new air mass is 1 m s^{-1} more than before, i.e. 1.68 m s^{-1} . From the glide polar, this corresponds to an air speed of 25.5 m s^{-1} and, if the gust velocity were sustained, the albatross would be able to accelerate to this speed without diving (neglecting energy lost in overcoming drag). The height to which the bird could pull up, if it could convert all of the kinetic energy gained from speeding up from 15.0 to 25.5 m s^{-1} into potential energy, is the kinetic energy height (h_k) from equation (8). If we set g to 9.81 m s^{-2} , then $h_k = 21.7 \text{ m}$. A sudden gust of only 1 m s^{-1} , coming from below, can supply a pulse of kinetic energy, sufficient to climb to a height typical of albatross pullups.

Relative direction of the gust

If the albatross of Figure 7 were to fly into a 1 m s^{-1} gust coming from directly ahead, its air speed would increase from 15 to 16 m s^{-1} , and the resulting kinetic energy height (equation 8) would be only 1.58 m , smaller by a factor of 13.7 than the kinetic energy height due to a gust of the same strength coming from below. This large difference in the energy gained is due to the difference in the gust direction relative to the bird, not its direction relative to the earth's surface. If we suppose that the image in Figure 6, of a glider about to enter a gust, came from a camera mounted on the wing tip, the image would look the same whether the glider is banked, or even upside down, so long as the direction of the gust is the same as before, relative to the glider. If a gust strikes the bird from its ventral side as shown, R increases in magnitude and rotates forwards as in Figure 6, irrespective of where the earth is relative to the bird.

To exploit separation bubbles over the ocean surface, the bird must manoeuvre in such a way that, as it crosses the boundary from light to strong wind, the stronger wind strikes it as squarely as possible from the ventral side. It has no control over the direction of the gust relative to the sea, so it has to achieve the proper orientation by rotating itself, presenting its ventral side to the direction from which the gust is expected to come, or from which it is detected. In the example above, the al-

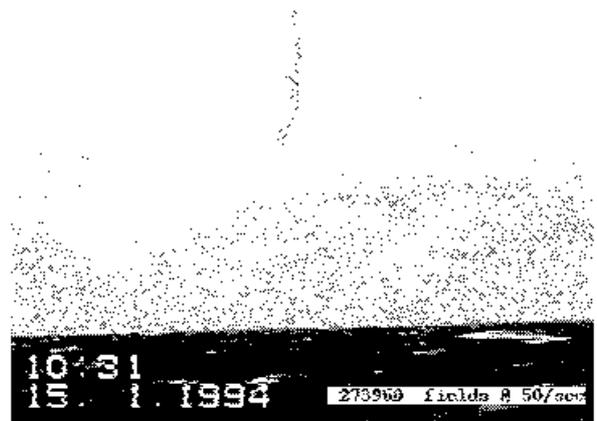


Figure 8. A black-browed albatross banking past the vertical at the top of a pullup. The bird's ventral side faces the wind, which is coming from the left. The double image is caused by interlacing two video fields, separated by 20 ms and each exposed for 1 ms , to make the frame.

batross flying into a horizontal gust of 1 m s^{-1} would get nearly 14 times as much energy by rolling belly-to-wind, as it would get if it received the same gust from directly ahead, with its wings level. A gust in turbulent air, especially in the lee of a ship or an iceberg, may actually have a downward component, and albatrosses are able to react so fast that they can roll past the vertical (over-bank) in response to this, even when close to the surface (Fig. 8). By pulling up, the albatross remains in the stronger wind for long enough to absorb the delayed effect of the surge (above), and maximise the kinetic energy gained. Depending on its direction of travel, the bird can turn into wind for another pullup, or use the energy gained for a prolonged glide into wind, in ground effect close to the surface.

Climbing with the wings level through a wind gradient, according to the classical theory, corresponds to receiving a succession of gusts from an unfavourable direction (ahead), which quickly become weak as the albatross climbs. It is only possible to maintain air speed in this way very close to the surface (above). Climbing or descending through the wind gradient is an ineffective way to exploit the energy available. Far more can be gained in the form of pulses of energy, by rolling belly-to-wind on encountering gusts near the surface.

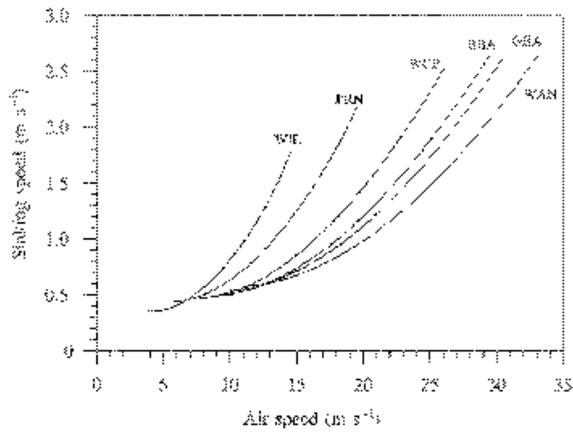
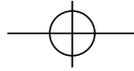


Figure 9. Computed glide polars for the species in Table 1 (parabola fit).

Species of different size

Smaller procellariiform species than albatrosses also pull up, but not so high, and the tiny storm-petrels were not seen pulling up at all. This can be understood from the relationship of the kinetic energy height gained from a gust of given strength to the shape of the glide polar. Figure 9 shows parabola approximations to computed glide polars for the six species in Table 1. In larger species, the curve expands upwards and to the right,

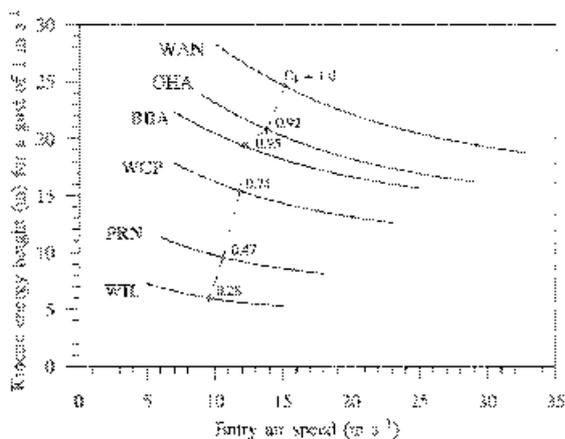


Figure 10. Kinetic energy height for a 1 m/s gust for the species in Table 1, as a function of entry air speed. The crosses show the mean air speed at which each species was observed flying over the sea by Pennycuick (1982), with the corresponding gliding lift coefficients.

as a direct result of the scaling of wing loading. The polars of the smaller species also curve upwards more steeply than would be caused by this effect alone, owing to the allometry of wing shape, whereby the aspect ratio is lower in smaller species (Pennycuick 1982). Applying the construction of Figure 7 to the different curves in Figure 9, it can be seen that a given gust velocity results in a smaller speed increase in small species than in large ones, and hence that a smaller species gets less kinetic energy height than a larger one. The kinetic energy height also depends on the slope of the polar, at the 'entry speed', that is the air speed at which the bird is flying when it enters the gust. The flatter the polar, the more speed is gained, for a given gust velocity. This also favours the larger species and, for any particular species, it favours a low entry speed. Figure 10 shows the kinetic energy height for each species, calculated as a function of entry speeds marked on the polars of Figure 9, for a gust of 1 m s^{-1} . The crosses represent the mean speed at which each species was observed flying over the sea by Pennycuick (1982), and the corresponding kinetic energy height, which varied from 6.0 m for Wilson's storm-petrel to 24.6 m for the wandering albatross. This graph is readily reconcilable with Figures 2 and 3, showing that albatrosses and large petrels pull up higher than prions, whereas storm-petrels get so little energy height from gusts that it is not worth their while to pull up at all, and they mostly proceed by flapping flight. Of course, it does not follow that storm-petrels do not soar. They may still gain energy by passing through the boundaries of separation bubbles, despite flapping while they are doing it.

Sensory requirements for gust soaring

If procellariiform birds extract energy from gusts by manoeuvring in and out of separation bubbles, then they must be able to monitor rapid changes in air speed. The air speed indicators of aircraft work by measuring the difference between the pressure in a forward-pointing 'pitot tube', and the 'static pressure' from a small hole, flush with the aircraft's skin. This pressure difference is called the 'dynamic pressure' (p), and it is related to the air speed (V) by the equation:

$$p = \rho V^2/2, \quad (9)$$

where ρ is the air density. The difficulty is that the dy-

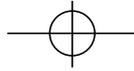


Figure 11. A. Wandering albatross *Diomedea exulans*, with separate, forward-pointing, scoop-shaped nostrils on the sides of the bill, typical of Diomedeidae. B. Giant petrel *Macronectes giganteus* with fused, tubular nostrils on the top of the bill, typical of Procellariidae.



dynamic pressure is rather small at bird speeds. The glide polars of Figure 9 suggest that medium-sized petrels may manoeuvre at speeds down to 8 m s^{-1} , and albatrosses down to 12 m s^{-1} . For the standard sea-level air density of 1.23 kg m^{-3} , the corresponding dynamic pressures would be about 40 and 150 N m^{-2} , or 4 and 9 mm of water. These are miniscule pressures, too small to be measured by a conventional aircraft air speed indicator. A specialised sense organ would be needed.

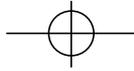
Procellariiform birds have a large and elaborate nasal sense organ, which is connected to the forward-pointing nostrils. It is separated by a septum from the mouth cavity, which could serve as a source for the static pressure, via the imperfectly sealed sides of the gape. Anatomists who have studied this organ, notably Bang (1966), invariably assumed that its function is olfaction, although experiments on the sense of smell (reviewed by Tickell 2000) gave positive results in some species but not in others. The organ may indeed be an olfactory organ but that would not exclude the possibility that it also contains mechanoreceptors that measure the distortion of the septum, caused by the small excess pressure in the nostril over that in the mouth cavity. Besides analysing smells, the large olfactory lobes of petrels and albatrosses, also mentioned by Tickell (2000), may serve to monitor dynamic pressure. As a hypothesis, I propose that the tubular nostrils of petrels, which are combined in a single tube, on the top of the beak (Fig. 11a), are the outward sign of a sensitive air speed sense. In albatrosses (Fig. 11b), which fly faster and therefore have larger dynamic pressures to measure, the nostrils are separate, and take the form of forward-pointing scoops on the sides of a deep, knife-like bill. If each nostril were an air speed sensor, this configuration could serve in addition as a yaw detector, meaning that

the difference in the dynamic pressure between the right and left nostrils would serve to inform the albatross whether the relative wind is coming from directly ahead, or angled right or left.

The procellariiform advantage

Tickell (2000), commenting on the tubular nostrils of Procellariiformes, commented: '... it cannot be said that we understand what they give to their possessors, that other seabirds do well enough without'. In winds of medium strength, say $10\text{--}20 \text{ m s}^{-1}$, the ocean surface is densely covered with separation bubbles, each one of which is a source of kinetic energy for birds, as Scorer (1958) observed (Fig. 5). I suggest that tubenosed birds have access to this unlimited supply of energy, while other seabirds do not. Pelecaniform birds (except frigatebirds, Fregatidae, which soar in thermals over the sea) have to budget a substantial fraction of their fuel energy for flapping flight when they migrate or forage, whereas Procellariiformes can travel almost free, and cover much longer distances than their pelecaniform counterparts. Northern gannets *Sula bassana* feeding young on the east coast of Britain make daily foraging flights up to about 400 km away (Nelson 1978). Even the more pelagic Red-footed Booby *S. sula* apparently forages within 250 km of the isolated nesting colony on Johnston Atoll in the Pacific (Ballance 1995). Such short and frequent foraging flights contrast with those of wandering albatrosses, which may range 10 times as far from their nesting islands (Prince et al. 1992, 1997, Weimerskirch et al. 1993).

There is no major difference in size or wing morphology between northern gannets and the smaller *Diomedea* albatrosses (mollymawks); indeed, inexpert nor-



them birdwatchers have been known to mistake errant albatrosses for gannets and vice versa. Both migrate and forage over the open sea, but their styles of flight could hardly be more different. Albatrosses skim low over the surface, pulling up abruptly and banking steeply from time to time. They do not need to gain speed before pulling up, by flying along the windward face of a wave in swell lift, as Wilson (1975) proposed to be the basis of their soaring. This variant of swell soaring (the marine counterpart of slope soaring) can be seen in American brown pelicans *Pelecanus occidentalis*, which often soar in small flocks along a wave in formation, and pull up in sequence before crossing downwind to the next wave. These pullups show neither the height nor the extreme angles of bank that are characteristic of albatross pullups. The same is true of gannets, which only pull up from the windward faces of waves, when travelling downwind. In any other direction, gannets and pelicans resort freely to flapping flight, whereas albatrosses flap their wings infrequently at sea. Gannets, pelicans and cormorants also sometimes fly in formation, but procellariiform birds never do so. Gust soaring depending on a specialised air speed sense, of which the tubular nostrils are the outward sign, would appear to be the key adaptation that gives procellariiform birds the freedom to roam anywhere over the oceans. Other seabirds are somewhat limited without it.

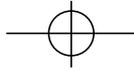
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Carotenoid derived plumage coloration in the siskin *Carduelis spinus* is related to foraging ability

Juan Carlos Senar and Diana Escobar

Because birds cannot synthesise carotenoid pigments and must obtain them from food, it has been suggested that carotenoid-based plumage coloration may be linked to nutritional condition, and hence, to foraging success or efficiency. Here we test this idea in the siskin *Carduelis spinus* by analysing the relationship between the length of the yellow wing stripe and (1) the calling rate of isolated individuals, as a measure of reduced exploratory and leadership capabilities, and hence of low foraging skills, and (2) how easily birds were attracted to a feeding area by live decoys, on the basis that birds attracted by decoys are those that rely on other foragers to find food ('local enhancement') rather than on their own foraging skills. The results showed that siskins with long yellow wing stripes gave fewer contact calls when isolated and were less often attracted by decoys than birds with short yellow wing stripes, which strongly suggests that the length of the yellow wing stripe is related to foraging skills. The size of the melanin-based black bib of the siskin, which is a signal of social dominance, was not related to either of these two measures of foraging ability, which suggests that these two kinds of pigments communicate different qualities of the bearer.

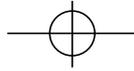
Key words: siskin, *Carduelis spinus*, carotenoid pigments, foraging skill.

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Birds cannot synthesise carotenoid pigments and must obtain them from their food (Goodwin 1973, Brush 1978, Hill 1992, Olson & Owens 1998). As a consequence, it has been suggested that carotenoid-based plumage coloration may be linked to nutritional condition, and hence, to foraging success or efficiency (Slagsvold & Lifjeld 1985, Hill & Montgomerie 1994, Hill 1999, McGraw & Hill 2000). However, most evidence obtained so far is only indirect. Hill & Montgomerie (1994) found for instance that carotenoid-based plumage brightness in house finches *Carpodacus mexicanus* was related to the growth rate of a male's tail feathers, suggesting that males with a brighter plumage are in better body condition, probably (but not proved) because of an enhanced foraging ability. Slagsvold & Lifjeld (1985) found that nestling great tits *Parus major* that were more frequently fed with caro-

tenoid enriched lepidopteran larvae, developed yellower plumage coloration, but these authors did not provide any data on the relationship between the colour of the parent birds and the kind of food supplied.

The aim of this work is to provide experimental data relating the extent of the carotenoid-based plumage coloration of siskins *Carduelis spinus* to their foraging ability. This is tested by two ways: (1) by analysing the relationship between the length of the yellow of the wing stripe and the calling rate of isolated individuals. High levels of vocalisation by an individual while isolated have been regarded as a sign of reduced exploratory and leadership capabilities, and hence of low foraging skills (Arnold 1977, Syme 1981, Beauchamp 2000). Therefore we predict that in the siskin there should be a negative correlation between the extent of yellow in the wing and calling rate of isolated indivi-



duals. (2) We investigate the relationship between the length of the yellow of the wing stripe and how easily birds are attracted to a feeding area by live decoys: we have elsewhere shown that birds attracted by decoys are those that rely on other foragers to find food ('local enhancement') rather than on their own foraging skills (Senar & Metcalfe 1988). We predict, therefore, that birds attracted by decoys, showing poorer foraging abilities, should display shorter yellow wing stripes than non-attracted birds. We chose siskins because their tame behaviour allowed us easily to record captive birds and because they will form a live decoy flock. The siskin has also the advantage of displaying both carotenoid and melanin-based plumage colours, which additionally allowed us to test for the different role of these two kinds of coloration in intraspecific communication (Hill & Brawner 1998, Badyaev & Hill 2000, McGraw & Hill 2000).

Material and methods

Siskins used in the experiments were captured in the suburbs of Barcelona, Spain. In this species, the yellow fringe of primaries 5–10 (numbered ascendantly) forms a yellow small patch on the wing. This yellow coloration is carotenoid-based (Stradi et al. 1995a, 1995b). In a sample of 19 birds, we measured for each primary 5–10, the length of the yellow from the distal edge of the overlying primary covert to the distal end of the yellow patch, which in fact is measuring the extent of yellow displayed by the bird to other flock companions. PC1 of a principal component analysis of the matrix re-

Table 1. Results of the principal components analysis (PCA) relating individuals ($n = 19$) to the length of the yellow area on each primary.

Primary	PC1
5	0.77
6	0.97
7	0.93
8	0.95
9	0.92
10	0.92
Eigenvalue	4.98
% Explained variance	83 %

Table 2. Regression between the number of contact calls given by isolated siskins in relation to the length of their carotenoid-based yellow wing stripe and the size of the melanin-based black bib, controlling for the age (yearling v. adult) of the bird. Beta coefficients refer to the slopes of the regression once variables have been standardised to a mean of 0 and a standard deviation of 1.

	Beta	Partial correlation	t_{28}	P
Yellow wing stripe	-0.45	-0.40	-2.31	0.03
Black bib	-0.16	-0.18	-0.95	n.s.
Age	0.21	0.20	1.07	n.s.

lating individuals to the length of the yellow at each primary summarised the size of the yellow wing patch (Table 1). However, given the high correlation of the yellow in primary 6 to PC1 and the ease of measuring just one primary, we used instead the length of the yellow in primary 6 alone as an accurate estimation of the size of the whole yellow patch. We also measured the length and width of the melanin-based black bib and calculated the 'badge area' (Senar & Camerino 1998), which is positively related to the dominance of an individual. Age was recorded according to Svensson (1992).

Siskins simultaneously captured in the same mist net were considered to belong to the same group. Each group (2–6 individuals) was maintained in the same cage (100 x 40 x 40 cm) visually and acoustically isolated from the other groups, for a month before starting the experiment to ensure acclimatisation to captivity. We measured the calling rate of isolated individuals in the laboratory by tape recording for 3 minutes a bird that was isolated from its group at a distance of 10 m. Only long distance contact calls (Oehler 1977) were used in analyses. We recorded a total of 32 males. The relationship between call frequency and the length of the yellow stripe and the size of the black bib was analysed by multiple rank correlation (Conover 1981). Since plumage coloration in the siskin is age-related (pers. obs.), we controlled for the age of the bird (yearling v. adult), by introducing this variable within the analysis.

In order to relate the size of the yellow wing stripe to a bird's readiness to be attracted by decoy birds, we set

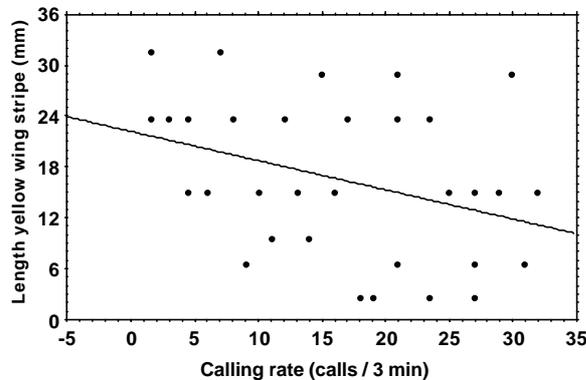
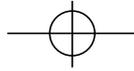


Figure 1. Relationship between the long distance calling rate of siskins and the length of the yellow wing stripe (measured on primary 6).

a mist net next to cages containing four tame siskins that frequently gave contact calls as they fed on the food within the cages, but with no food available outside the cages. At the same time we placed a platform trap, acting as a permanent feeding station, 45 m from the mist net. The experimental procedure was identical to that of Senar & Metcalfe (1988). Wintering populations of siskins may include both resident and transient birds (Senar et al. 1992). Since residents are rarely attracted by decoys (Senar & Metcalfe 1988), we used only transient birds (i.e. birds captured only once in the study area and never recaptured). Definition of residence status was done *a posteriori*, so that transients, by definition, were those birds captured only once during the winter; if an experimental bird was captured after its first capture, it was deleted from the results. Winter ab-

Table 3. Logistic regression showing the relationship between the probability of a siskin being attracted by live decoys (i.e. relying on local enhancement to find food) in relation to the length of the carotenoid-based yellow wing stripe and the size of the melanin-based black bib, controlling for the age of the bird (yearling vs. adult), and the year (irruptive v. average abundance of siskins).

	Wald statistic	d.f.	P
Yellow wing stripe	4.24	1	0.04
Black bib	1.66	1	n.s.
Age	3.37	1	n.s.
Year	109.50	1	<0.001

undance of siskins is very variable from year to year (Newton 1972), so that winters can be classified according to whether siskin irruptions occurred (birds very abundant) or did not occur. In order to avoid any bias related to the abundance of siskins, the dataset was divided between irruptive (1996–97; $n = 196$ birds) and non-irruptive (1993–96, 1997–98, $n = 161$ birds) winters. Data were analysed by logistic regression, and we controlled for the abundance of siskins (irruptive v. non-irruptive winter) and the age of the birds (yearling v. adult) by introducing these two variables within the analyses.

Results

After controlling for the age of the birds, the calling rate of experimentally isolated siskins showed a significant negative relationship to the size of the yellow wing stripe, as measured on primary 6 (Fig. 1, Table 2), but not to the size of the black bib of the bird (Table 2).

After controlling for the age of the birds and their abundance (irruption effect), the probability of a siskin being attracted by live decoys was affected by the size of its yellow wing stripe but not by the size of the black bib (Table 3): birds attracted by decoys showed shorter yellow wing stripes than birds using the feeding station (Fig. 2). We additionally found that siskins were more often trapped in the mist nets near the decoys in non-irruptive years than in irruptive ones. However, this was an artefact of the trapping scheme, in that the great ac-

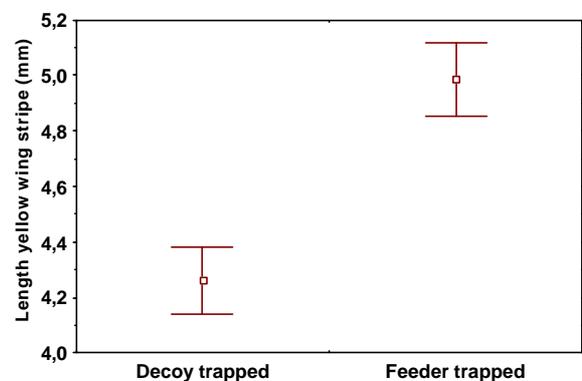
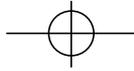


Figure 2. Length (mean \pm s.e.) of the carotenoid-based yellow wing stripe of male siskins attracted to live decoys versus male siskins trapped at bird tables.



tivity of resident siskins at the feeders in irruptive years probably attracted many birds that would be otherwise have been attracted by decoys. Because of this winter abundance effect, we computed whether there was any interaction between the size of the yellow wing stripe and year (irruptive v. non-irruptive), but this was not significant (Wald statistic = 0.22, $P = 0.64$), and did not have any effect on the significance of the size of the wing stripe (Wald statistic = 4.14, $P = 0.04$). The size of the wing bar did not vary between irruptive and non-irruptive years ($F_{1,516} = 1.01$, n.s.). There was some marginal effect of age (Wald statistic = 3.37, $P = 0.07$), in that yearlings tended to be less attracted by decoys. However, this was also probably an artefact of the trapping scheme in that in irruptive years, yearling birds are more abundant than adults, and in these years siskins are less often captured with decoys because birds at feeders also attract them.

Discussion

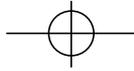
There is current interest in whether the two main pigments responsible for bird coloration (i.e. carotenoids and melanin (Brush 1978)) might convey different kinds of information about the bearer (Hill & Brawner 1998, Figuerola et al. 1999, Badyaev & Hill 2000, McGraw & Hill 2000). Because carotenoids can only be obtained by animals indirectly through their food, it has been suggested that this coloration might serve as an honest signal of foraging ability and overall condition (Hill 1991, Gray 1996, Hill & Brawner 1998, Olson & Owens 1998, Badyaev & Hill 2000, McGraw & Hill 2000). Conversely, melanin based coloration seems to be more closely related to the signalling of social dominance (Senar 1999, González et al. 1999, McGraw & Hill 2000; see however Maynard Smith & Harper 1998 for the carotenoid derived signal related to social status in greenfinches *Carduelis chloris*). Our results support this view: the carotenoid-based yellow wing stripe of the siskin was related to foraging ability, whereas the melanin-based black bib has been shown elsewhere to be a signal of dominance status (Senar et al. 1993, Senar & Camerino 1998).

Nevertheless, apart from very general arguments relating the acquisition of carotenoids to their expression, the underlying mechanism responsible for the relationship between the length of the yellow wing stripe

and foraging behaviour is still unknown. The view of carotenoids as 'rare' compounds (Olson & Owens 1998) supports the hypothesis that some birds are brighter because they are better foragers and hence ingest larger quantities of carotenoids. However, the yellow in the siskin yellow wing stripe is formed from the oxidation of lutein, which is a quite common carotene in nature (Stradi 1998). Hence we should perhaps favour the view that the general 'quality' of the individual affects both its plumage colour and foraging efficiency, perhaps via physiological processes (Møller et al. 2000). The lack of association between dominance (i.e. black bib size) and foraging ability is consistent with the experiments of Wiley (1991) on the white-throated sparrow *Zonotrichia albicollis*, who found that the ability to locate novel locations of food was not related to social status, and stresses that dominance does not always entail advantages and that the ability to monopolise or scrounge food is not necessarily related to the ability to find this food.

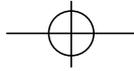
The adaptive function of multiple messages in animals is a topic of great theoretical interest (Møller & Pomiankowski 1993, Johnstone 1996) and has been the subject of recent empirical studies (Brooks & Coudridge 1999, McGraw & Hill 2000). The siskin appears to provide an ideal model species for testing the adaptive function of multiple signals in animals, because the two kinds of ornaments (carotenoid and melanin-based) appear within the same species and we have been able to identify different functions for each.

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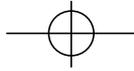
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Differential reproductive success of great spotted cuckoos *Clamator glandarius* parasitising magpies *Pica pica* and carrion crows *Corvus corone*: the importance of parasitism costs and host defences

Manuel Soler, Juan J. Soler, Tomás Pérez-Contreras and Juan G. Martínez

We investigated differences in the reproductive success of great spotted cuckoos *Clamator glandarius* and fitness costs of parasitism for their primary host, the magpie *Pica pica* (slightly larger than the cuckoo and showing defensive mechanisms against the parasite), and their secondary host, the carrion crow *Corvus corone* (more than twice the size of the cuckoo, but lacking defensive mechanisms). Because carrion crows started laying before magpies, and the laying season of great spotted cuckoos was longer than either of their hosts', they were able to parasitise both hosts. Hatching success of the parasite was higher in carrion crow than in magpie nests, but fledging success was significantly higher when parasitising magpies than carrion crows. The cost to the hosts of successful parasitism was twice as high in magpie (3.0 fewer magpie nestlings fledged in parasitised compared to unparasitised nests) as in carrion crow nests (1.5 fewer nestlings). Fledging success of great spotted cuckoos was lower in carrion crow nests because nestlings of this host species had a superior competitive ability compared to cuckoo chicks due to their larger size. This also explained why the cost of parasitism was lower for carrion crows than magpie hosts. The larger carrion crow host provided the cuckoo chick with more food than it can eat, and there is thus always enough food for late-hatched host chick(s) that soon become larger and, hence, out-compete the cuckoo chick. The low cost of parasitism for carrion crows explains why this host species has not developed defensive mechanisms.

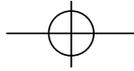
Key words: brood parasite, host defence, great spotted cuckoo, reproductive success.

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Avian brood parasites should not parasitise unsuitable hosts. Most species of brood parasite appear to avoid hosts that are likely to reject their eggs, that are too small or too large, or that feed their nestlings with food inappropriate for parasitic nestlings (Rothstein 1990). Host preferences must be related to differences in fitness obtained by parasitism on different hosts, and certain host characteristics may be responsible for such differential parasite fitness. If brood parasite fitness increases when using hosts of a particular phenotype, natural selection will favour individual parasites selec-

ting hosts with this phenotype (Price 1980). However, generalist brood parasites of the genus *Molothrus* (cowbirds) sometimes parasitise some host species despite the fact that never or only rarely fledge parasites (Scott 1977, Fraga 1985, Friedmann & Kiff 1985, Kozlovic et al. 1996).

Recently, in a comparative study of host selection in the European cuckoo *Cuculus canorus*, Soler et al. (1999a) provided evidence suggesting that host availability in time (duration of the breeding season) and space (relative population size), as well as the duration



of the nestling period of potential hosts relative to their body size, explained host selection by this parasitic cuckoo. The European cuckoo has been reported to parasitise more than 50 host species in Britain, but three of these species accounted for 77 % of all cases of parasitism (Glue & Morgan 1972). Although it is clear that the European cuckoo selects particular species as hosts (Glue & Morgan 1972), no study has yet analysed in this or any other parasitic cuckoo-host system the differential breeding success of the cuckoo when parasitising different host species (but see Soler 1990 for a preliminary analysis).

The parasitic cuckoo chick most commonly evicts the host eggs or chicks from the nest, thus reducing the reproductive output of the host to zero. However, in some species the cuckoo chick does not evict host offspring, leaving the hosts a chance to rear some of their own nestlings, as it is the case in cuckoos of the genus *Clamator*.

The great spotted cuckoo *Clamator glandarius* is a specialist that only occasionally parasitises more than one host species. In the Palearctic, its primary host is the magpie *Pica pica* and its secondary host is the carrion crow *Corvus corone* (Cramp 1985, Soler 1990). In Egypt great spotted cuckoos also use the carrion crow as their primary host but use magpies in northwest Africa (Cramp 1985, Fry et al. 1988). In sub-Saharan Africa the most frequently recorded host is the pied crow *C. albus* but the black crow *C. capensis*, African pied starling *Spreo bicolor*, red-winged starling *Onychognathus morio* and pale-winged starling *O. nabeourou* are also used (Rowan 1983, Fry et al. 1988).

In Spain, the great spotted cuckoo parasitises magpies (Alvarez & Arias de Reyna 1974, Arias et al. 1982, Soler 1990), carrion crows (Valverde 1953, Soler 1990) and, sporadically, choughs *Pyrrhonorax pyrrhonorax* (4.9 %) and jackdaws *C. monedula* (2.1 %) (Soler 1990). Magpies, which are about half the size of the carrion crow (Cramp & Perrins 1994), are used preferentially as hosts: in one study 30 out of 69 (43.5 %) magpie nests, and only 4 out of 47 (8.5 %) carrion crow nests were parasitised (Soler 1990).

Brood parasitism by the great spotted cuckoo strongly affects the breeding success of its magpie host. On average only 0.6 magpie chicks fledge per parasitised nest, whereas 3.5 magpie chicks fledge from unparasitised nests (Soler et al. 1996). The reproductive failure of the magpie is mainly caused by egg destruction by

adult cuckoos, but also by nestling cuckoos out-competing magpie chicks, especially when the cuckoo nestling hatches several days before magpie nestlings (Soler et al. 1996). However, when the cuckoo egg is laid after clutch completion, the cuckoo hatches at the same time or after the host nestlings, reducing the breeding success of the cuckoo and the cost of parasitism for magpies considerably (Soler 1990, Soler et al. 1996, Soler et al. 1997).

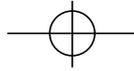
Magpies respond aggressively towards adult great spotted cuckoos and they reject cuckoo eggs laid in their nests (Alvarez et al. 1976, Arias et al. 1982, Soler 1990, Soler & Møller 1990, M. Soler et al. 1999). Carrion crows do not attack great spotted cuckoos (Soler et al. personal observation) and do not reject even strongly non-mimetic eggs (Yom-Tov 1976, Soler 1990). In a previous study we found that more great spotted cuckoos fledged from magpie nests than from carrion crow nests, but only four parasitised crow nests were examined (Soler 1990).

In this paper we compare the reproductive success of great spotted cuckoos parasitising magpies and carrion crows, and calculate the fitness costs of parasitism on these host species. We ask two questions: first, why is the breeding success of great spotted cuckoos higher when parasitising magpies, the host species with anti-parasite defences, than when parasitising carrion crows, which lacks defences and feeds young large amounts of food? Second, why has the carrion crow never developed defences against the parasite despite long being used as a host by the great spotted cuckoo?

Materials and Methods

Field work was carried out mainly between 1993 and 1997 in Hoya de Guadix, southern Spain (37° 18' N, 3° 11' W), a plateau at an altitude of 1000 m a.s.l. with cultivated cereals (especially barley), and many groves of almond trees *Prunus dulcis* and some groves of holm oaks *Quercus rotundifolia*. Magpies nested preferentially in the almond groves and carrion crows in the holm oak habitat.

We found 144 carrion crow nests, 41 (28.5 %) of which were parasitised by great spotted cuckoos. We have performed several field experiments in magpie nests during other studies but, in this study, we included data only from non-experimental nests. Of 357



magpie nests, 199 (55.7 %) were parasitised. More detailed information on the frequency of parasitism in magpies by year and study plot is given in Soler et al. (1998). To avoid the effect of nest predation when analysing the breeding success of great spotted cuckoos and hosts (magpies and carrion crows), only successful nests (those in which at least one chick fledged) were used in the analyses. Furthermore, to avoid the effect of habitat and year in the analyses of reproductive parameters, we considered only successful nests of both species studied during 1993–1997 in the almond tree habitat. Thus, in these analyses we have used a total of 239 magpie nests (142 parasitised, 59.4 %) and 54 carrion crow nests (33 parasitised, 61.1 %). However, a potential habitat effect will be considered in relation to parasitism rate.

We inspected nests at least once or twice per week, and daily during laying and hatching. Multiple parasitism by one or more adult great spotted cuckoo females was determined on the basis of differences in the appearance of cuckoo eggs and laying dates, a method that has been demonstrated to be quite accurate (Martínez et al. 1998). Breeding parameters such as laying date, clutch size, number of eggs hatched, and number of fledglings were not recorded in all nests. Thus sample size is not the same for all variables. Clutch size was considered as the maximum number of magpies or carrion crow eggs observed in the nest, although some host eggs could have been damaged by cuckoos and remo-

ved by hosts before the next nest inspection (Soler et al. 1997, M. Soler et al. 1999). The number of eggs hatched was estimated as clutch size minus unhatched eggs (eggs destroyed by the parasite were considered as unhatched eggs). Hatching success was the mean percentage of eggs hatched, fledging success was the mean percentage of fledglings and breeding success was the mean percentage of eggs that produced fledglings.

Analyses of hatching, fledging, and breeding success treated each nest as an independent data point. We have used non-parametric statistics because variables did not fit conditions for parametric tests (Siegel & Castellan 1988). Values are means \pm s.e.

Results

Parasitism frequency and laying season of magpies and carrion crows

In the holm oak groves, the habitat preferentially used by carrion crows, we found 81 carrion crow nests of which 6 (7.4 %) were parasitised by the great spotted cuckoo. In this habitat, during the same period, only 32 magpie nests were found but 17 (53.1 %) were parasitised. Parasitism frequency was significantly lower for crows than for magpies ($\chi^2 = 29.57$, $df = 1$, $P < 0.00001$). In the almond habitat, during 1993–1997 we found 63 carrion crow nests, of which 35 (55.6 %) were parasitised by great spotted cuckoos. During the same period, we found 325 magpie nests, 182 (56 %) of which were parasitised. Parasitism frequency was similar in the two host species in this habitat, the one preferentially used by the magpie ($\chi^2 = 0$, $df = 1$, $P = 0.95$). Considering parasitism rate independently of the habitat, parasitism on magpies (55.7 %) was higher than on carrion crows (28.5 %) ($\chi^2 = 31.18$, $df = 1$, $P < 0.00001$). Furthermore, we consider the magpie to be the primary host because in the almond habitat between 1993 and 1997 great spotted cuckoos laid a total of 384 eggs in magpie nests and 54 in carrion crow nests.

Carrion crows began to breed about three weeks earlier than magpies in the same habitat (Fig. 1). The laying season of great spotted cuckoos coincided with that of magpies, so that magpies were parasitised throughout their laying period, whereas carrion crows were parasitised only during the second half of their laying period.

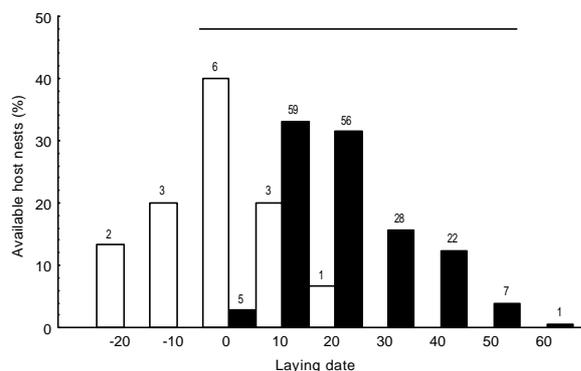


Figure 1. Percentage of available host nests of magpies (black bars, $n = 178$) and carrion crows (white bars, $n = 20$) in 10-day periods (1 = 1 April). Numbers above bars are available host nests. Line above histogram represent great spotted cuckoo laying season.

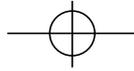


Table 1. Breeding success of great spotted cuckoos in magpie and carrion crow nests. Mann-Whitney U-test, probability levels: * $P < 0.025$, ** $P < 0.005$.

	Magpie			Carrion crow		
	Mean	s.e.	n	Mean	s.e.	n
Number of parasitic eggs per nest	2.1	0.1	140	1.8	0.1	29
Number of parasitic females laying per nest	1.3	0.06	122	1.3	0.1	23
Number of eggs hatched	1.7	0.1	137	1.8	0.1	33
Number of unhatched eggs	0.4	0.06	135	0.07	0.06	29*
Number of chicks fledged	1.5	0.08	141	1.3	0.1	33
Number of dead chicks	0.2	0.04	137	0.5	0.1	33**

Differential reproductive success of great spotted cuckoos

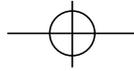
Most variables related to the reproductive success of great spotted cuckoos were very similar when parasitising both magpies and carrion crows (Table 1). However, the hatching success of great spotted cuckoos was significantly higher in carrion crow than in magpie nests (Fig. 2, Mann-Whitney U-test, $z = -2.12$, $P = 0.03$). The opposite result was found for fledging success: the percentage of cuckoo chicks that fledged was significantly higher when parasitising magpies than when parasitising carrion crows (Fig. 2, Mann-Whitney U-test, $z = -2.96$, $P = 0.003$). Overall, breeding success was higher in magpie than in carrion crow nests, although the difference was not statistically significant (Fig. 2, Mann-Whitney U-test, $z = -1.3$, $P = 0.19$).

Different fitness costs of parasitism for magpies and carrion crows

Parasitism by great spotted cuckoos drastically affected the reproductive output of magpies (Table 2). Hatching, fledging and breeding success of magpies were all considerably higher in non-parasitised than in parasitised nests (Fig. 3; Mann-Whitney U-test, $P < 0.00001$ in the three cases). Likewise, in carrion crows the number of eggs hatched and the number of chicks fledged were significantly higher in non-parasitised than in parasitised nests (Table 3). Hatching and breeding success were also significantly higher in non-parasitised than in parasitised nests (Fig. 3, Mann-Whitney U-test, $z = -3.83$, $P = 0.0001$; and $z = -3.42$, $P = 0.0006$, respectively), but the percentage of carrion crow chicks that survived to fledging in parasitised and unparasitised nests was not significantly different (Fig. 3, Mann-Whitney U-test, $z = -0.9$, $P = 0.39$).

Table 2. Breeding success of magpies in parasitised and unparasitised nests. Mann-Whitney U-test, probability levels: * $P < 0.00001$.

	Parasitised nests			Unparasitised nests		
	Mean	s.e.	n	Mean	s.e.	n
Number of eggs per nest	5.6	0.1	142	6.9	0.1	97*
Number of eggs hatched	1.7	0.2	123	5.5	0.2	89*
Number of unhatched eggs	3.8	0.06	123	1.4	0.03	89*
Number of chicks fledged	0.7	0.1	140	3.6	0.1	94*
Number of dead chicks	1.1	0.04	122	1.9	0.1	86*



All parameters related to loss due to parasitism were significantly higher in parasitised magpie nests than in parasitised carrion crow nests (Tables 2 and 3; Mann-Whitney U-test; number of eggs unhatched, $z = -3.9$, $P = 0.00009$; number of chicks dead, $z = -2.2$, $P = 0.02$). Overall, the number of chicks fledged was significantly lower in magpie than in carrion crow nests (Mann-Whitney U-test, $z = -5.4$, $P < 0.00001$), even though clutch and brood size of magpies are larger than those of carrion crows. The average cost of successful parasitism was therefore almost twice as high in magpie nests (3.0 fewer nestlings fledged in parasitised compared to unparasitised nests) as in carrion crow nests (1.5 fewer nestlings).

Discussion

Host selection

Some cuckoo females in our study area may use carrion crows as well as magpies as hosts. In a previous study using genetic markers we found that one great spotted cuckoo female laid four eggs in the nests of carrion crows and six eggs in magpie nests (Martínez et al. 1998). The results of the present study show, however, that the cuckoo laying season is synchronised with that of the magpie, and that carrion crows, which begin breeding earlier, are parasitised only as secondary hosts at the beginning of the cuckoo breeding season when few magpie nests are available.

It has been suggested that cuckoos may be habitat specific with regard to their laying area (Teuschl et al. 1998). If so, the different parasitism rates in our two habitats could be explained by habitat specificity alone:

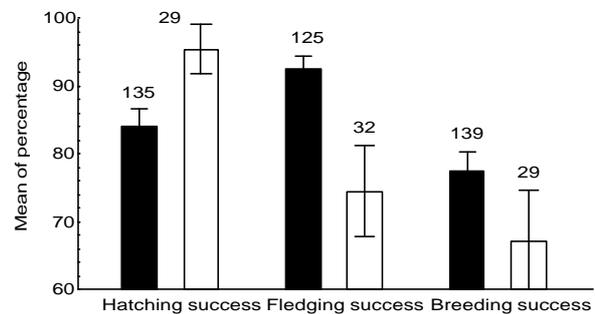


Figure 2. Hatching, fledging, and breeding success of great spotted cuckoos in the nests of magpies (black bars) and carrion crows (white bars). Values are means \pm s.e. Numbers above bars are sample sizes.

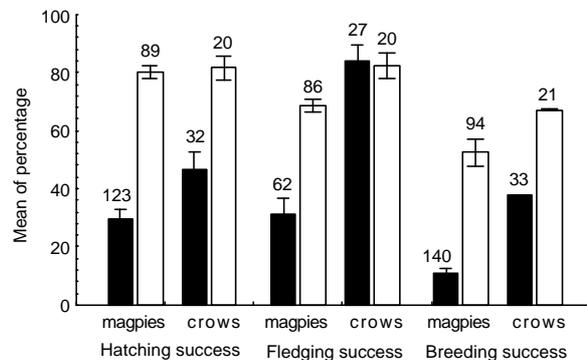
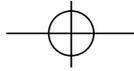


Figure 3. Hatching, fledging, and breeding success of magpies and carrion crows in parasitised (black bars) and unparasitised nests (white bars). Values are means \pm s.e. Numbers above bars are sample sizes.

'oak cuckoos' may just be rarer than 'almond cuckoos'. However, this is unlikely because: (1) parasitism rate of magpies in the oak habitat is as high as in the almond

Table 3. Breeding success of carrion crows in parasitised and unparasitised nests. Mann-Whitney U-test, probability levels: * $P < 0.005$, ** $P < 0.00005$.

	Parasitised nests			Unparasitised nests		
	Mean	s.e.	n	Mean	s.e.	n
Number of eggs per nest	4.2	0.2	33	4.6	0.2	21
Number of eggs hatched	1.9	0.2	32	3.7	0.2	20**
Number of unhatched eggs	3.4	0.3	32	0.9	0.2	20*
Number of chicks fledged	1.6	0.2	33	3.1	0.3	21**
Number of dead chicks	0.3	0.1	32	0.6	0.1	20



habitat (see above), and (2) great spotted cuckoo females provided with radio-transmitters visited both habitats (Soler et al. unpubl.).

Why is the breeding success of the great spotted cuckoo higher when using a magpie host?

Great spotted cuckoos parasitising carrion crows gain the advantage of nearly all their eggs hatching successfully, but that is not the case when parasitising magpies (Fig. 2). The difference arises from the different incubation periods of magpies (17.1 days, Arias et al. 1982); and carrion crows (20.7 days, Arias de Reyna 1998). With an incubation period in great spotted cuckoos of c. 13–14 days (Alvarez & Arias de Reyna 1974), a higher synchronisation of cuckoo and host laying dates is necessary when parasitising magpies than carrion crows. A failure to synchronise can give rise to late laying of a cuckoo egg, which is the main factor explaining hatching failure of great spotted cuckoos parasitising magpies, because female magpies stop incubating 4–7 days after the first chick has hatched (M. Soler et al., pers. obs.).

When parasitising magpies, great spotted cuckoo nestlings are of equal size and develop more quickly than magpie nestlings (Soler & Soler 1991). This is essential for nestling cuckoos to be fed preferentially by the magpie foster parents (Soler et al. 1995). When parasitising carrion crows, however, the much larger size of this host provides two clear advantages to the carrion crow nestlings in competition with cuckoo chicks. First, the adult crows provide the cuckoo chick with more food than it can eat, so there is always enough food for late-hatched host chicks. Second, the carrion crow chicks soon become larger than the cuckoo chick, which then loses its greatest advantage.

The percentage of cuckoo chicks that fledged was significantly lower when parasitising carrion crows than when parasitising magpies (Fig. 2). When great spotted cuckoo nestlings were reared without carrion crow nestlings ($n = 6$), however, all chicks survived to fledge, even when there was more than one cuckoo chick per nest ($n = 4$). These results imply that cuckoo chicks are frequently outcompeted by the much bigger carrion crow nestlings. Similarly, parasitic cowbirds of the genus *Molothrus* suffer a reduction in breeding success when using larger hosts, because cowbird chicks usually starve (Fraga 1978, 1985, Gochfeld 1979, Lich-

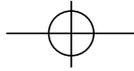
enstein 1998, Lorenzana & Sealy 1999). Great spotted cuckoos therefore gain greater reproductive success by parasitising magpies, but when magpie nests are unavailable, they use secondary carrion crow hosts.

Why has the carrion crow not developed defensive mechanisms against the parasite?

The lack of host defences against brood parasites can be explained by two different hypotheses: the 'evolutionary lag' and the 'evolutionary equilibrium' hypotheses (Rothstein 1990). The 'evolutionary lag' hypothesis (Rothstein 1982, 1990) states that defences would be adaptive and would spread among the population by natural selection as soon as they appeared, but that the necessary genetic variants have not yet arisen. Alternatively, the 'evolutionary equilibrium' hypothesis (Rohwer & Spaw 1988, Lotem et al. 1992, 1995) posits that defence behaviour has costs greater than non-defensive behaviour, and it is therefore less beneficial.

Selection pressures arising from parasitism may result in the evolution of host defences, but this outcome depends on two main factors: (1) the duration of sympatry between host and parasite and (2) the magnitude of costs imposed by brood parasitism. The duration of sympatry between the brood parasite and its hosts determines the development and the efficacy of host defence strategies (Soler & Møller 1990, Briskie et al. 1992, Davies & Brooke 1998, Soler et al. 1999b). Thus, a possible explanation for the lack of defences against the great spotted cuckoo in the carrion crow could be that this species has been used as a host by the cuckoo only recently. This seems unlikely because the carrion crow is the primary host of the great spotted cuckoo in Egypt (Cramp 1985, Fry et al. 1988), though unfortunately there is no information about defensive mechanisms used by carrion crows in Egypt. Moreover, parasitism by this cuckoo on carrion crows was documented in Spain about 50 years ago (Valverde 1953). Considering that magpies were able to increase rejection rate of non-mimetic eggs from about 50 % to nearly 100 % and that of mimetic eggs from 10 % to 50 % in only 12 years (Soler & Soler 2000), we can assume that carrion crows have apparently been exposed to cuckoo parasitism sufficiently long to develop defensive strategies against the brood parasite.

The 'evolutionary equilibrium' hypothesis suggests that in species with no recognition ability, the costs of



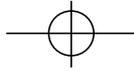
developing defences should outweigh the benefits (Rohwer & Spaw 1988, Lotem et al. 1992, 1995). The cost of parasitism directly affects the strength of selective pressures favouring the evolution of host defences. The cost of parasitism to carrion crows was about 1.5 fewer young fledged per nest, whereas in magpie nests 3.0 fewer chicks fledged. Perhaps the absence of defensive mechanisms in the carrion crow is attributable to the relatively small costs resulting from great spotted cuckoo parasitism, because parasitised individuals are able to rear most of their own young. Large hosts of the parasitic brown-headed cowbird *Molothrus ater* are also able to raise their own chicks (Ortega & Cruz 1988, 1991, Weatherhead 1989).

Given the low costs of cuckoo parasitism on carrion crows and its relatively infrequent occurrence, parasitism by the great spotted cuckoo may not constitute a sufficiently strong selection pressure for anti-parasitic defences to evolve in the carrion crow, supporting the 'evolutionary equilibrium' hypothesis.

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