The role of nest site cover for parental nest defence and fledging success in two *Acrocephalus* warblers

Sonia Kleindorfer[1], Birgit Fessl[2] and Herbert Hoi[2]

This study investigates nest defence and fledging success in relation to nest concealment in two closely related, socially monogamous *Acrocephalus* warblers: the moustached warbler *Acrocephalus melanopogon* and the reed warbler *Acrocephalus scirpaceus*. We test predictions of the nest exposure hypothesis, and propose that nest defence represents dynamic risk assessment as a function of nest concealment and predator type. During the late nestling feeding phase we placed one of three predator types (plastic snake, stuffed stoat, stuffed harrier) at 1 m from the nest. Nest defence was calculated as a composite factor score using: (i) number of alarm calls, (ii) latency to approach, and (iii) minimum distance to approach. In the moustached warbler, nest concealment was negatively associated with predation, whereas no effect was found in the reed warbler. Nest defence differed significantly in relation to the interaction effect between nest concealment and predator type. In both species, nest defence to the snake was highest at exposed nests from below and decreased with increasing nest cover. In the moustached warbler, a similar pattern was found for nest concealment from above, with higher defence to snakes and stoats at exposed nests. There was no observable variation in response to the harrier. In the reed warbler, reaction scores hardly differed between predator types in relation to nest concealment from above. Finally, in the moustached warbler, the level of nest defence was positively related to fledging success, but not in the reed warbler. These results provide partial support for the nest exposure hypothesis, as birds showed modified defence responses to different cases of nest concealment and predator type. The results also point to the possible role of behaviour in modifying predation outcomes for different cases of nest concealment.
Key words: nest concealment, nest defence, predation, fledging success, *Acrocephalus.*

[1]Flinders University of South Australia, School of Biological Sciences, GPO Box 2100, Adelaide 5001, Australia; [2]Konrad Lorenz Institute for Comparative Ethology, Savoyenstrasse 1a, A–1160 Vienna, Austria. Corresponding author: sonia.kleindorfer@flinders.edu.au

Nest predation is considered a prime determinant of avian reproductive success (Ricklefs 1969, Martin 1992, 1993a,b) and natural selection should favour habitat and nest site selection that reduces predation risk (Martin 1998). Habitat preferences for nest site location have been shown to be adaptive in birds, in that they are often associated with reduced predation levels (Martin 1998, Mermoz & Reboreda 1998, Schmidt et al. 1999, Misenhelter & Rotenberry 2000, Larison et al. 2001). Specifically nest concealment, that is the per-centage of vegetation cover surrounding the nest site, has been shown to be negatively correlated with nest predation in numerous studies (e.g. Martin 1993a, Hatchwell et al. 1996, Burhans & Thompson 1998, Eising et al. 2001). Some bird species may in fact be selected to trade-off between nest concealment (to avoid predation) and nest visibility (to monitor neighbors and potential threats) (Gotmark et al. 1995, Murphy et al. 1997, Wiebe & Martin 1998, Clarke et al. 2001). Behavioural compensation in the form of increased
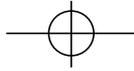
parental defence by parents at visually conspicuous nests has rarely been reported (but see Cresswell 1997, Murphy et al. 1997) and forms the focus of this study.

During predator encounters at the nest site, the level of nest defence by attending birds is predicted to be influenced by the perceived threat of the predator either to the brood or to the adult (Ghalambor & Martin 2000). We posit that this perceived risk should also be influenced by the level of nest site cover, with higher nest defence shown at conspicuous nests. Observed nest defence levels are therefore the result of an interaction between predator type and prey vulnerability. In a model proposed by Schmidt (1999), it is predicted that nest site characteristics influence predation susceptibility by changing nest encounter rates and predator recognition time. Schmidt (1999) further proposed that behavioural factors are important, but hitherto neglected, determinants of actual predation events in relation to nest site. This study focuses on behavioural variation in nest defence in relation to nest site cover (Cresswell 1997) and predator type (Halupka 1999) to test predictions of the nest exposure hypothesis. According to this hypothesis, anti-predator defence behaviour is positively associated with the probability of predator detection and is therefore highest at conspicuous nests.

Indications that parents may be compensating for nest location stem from Cresswell (1997) who showed in an experimental study that artificial nests were taken by predators according to detectability, whereas no effect of nest location on predation was found at natural nests with defending parents. Evidence of behavioural modification in response to nest concealment also comes from Halupka (1998) who showed in meadow pipits *Anthus pratensis* that, while fledging success was not related to nest concealment, nestlings at exposed nests fledged earlier than nestlings at hidden nests.

In this study we test predictions of the nest exposure hypothesis, and ask whether birds show adaptive defence tactics in relation to nest concealment and predator type. The predictions include the following: (i) a negative statistical association between nest concealment and predation; (ii) a negative statistical association between nest concealment and nest defence level; (iii) nest defence level varies in relation to the interaction effect between nest concealment and predator type – we assume that predator search strategies differ according to nest characteristics and pose different levels of threat (Martin 1988a,b,c), i.e. snakes pose a greater threat

to conspicuous ground-nests, stoats to conspicuous mid-reed nests, and harriers to conspicuous upper-reed nests; and (iv) a positive statistical association between parental nest defence and fledging success.

We used three predator types (plastic snake, stuffed stoat and stuffed harrier), which were experimentally placed at nests of the moustached warbler *Acrocephalus melanopogon* and reed warbler *A. scirpaceus* late during the period of nestling feeding. We consider the experimental predator types used in the study to be appropriate as they represent three common predators at the breeding site, including marsh harrier *Circus aeruginosus*, stoat *Mustela erminea*, and grass snake *Natrix natrix* (Hoi & Winkler 1988, 1991, 1994). These predators were selected based on previous experimental work, in which direct predator observations were made or predator type was inferred from egg marks and patterns of partial brood loss (Hoi & Winkler 1988, 1994).

Methods

Study site and species

This study was conducted in a marsh area around Lake Neusiedl in eastern Austria (47°56' N, 16°45' E) in spring 1994. The data set comprises 20 moustached warbler nests and 20 reed warbler nests. At least one parent at each nest was mist-netted and color banded. In the incubation or early feeding phase, hides were set up at distances of 4–5 m from the nest. We reorded the dates of the start of incubation, hatching, fledging, and any predation events.

The study species are both reed-dwelling warblers of similar size and ecology (Leisler & Catchpole 1992). They are ideal for such an investigation because they breed in overlapping territories yet differ in their nest placement within the reeds. Nest placement in moustached warblers occurs preferentially in the lower third of the vegetation (0–0.5 m), whereas it is in the mid-third (0.3–1.5 m) in reed warblers (Leisler 1991, Schulze-Hagen 1991, Hoi et al. 1995). In a previous study, predation levels were calculated as 40.4 % in moustached warblers and 50.7 % in reed warblers (Kleindorfer et al. 1997).
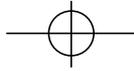
Measuring nest site characteristics

We measured the nest height (m from ground to nest rim) for all focal nests. We also measured the following habitat variables at the nest site: (i) reed height (mean of six samples at 2 m from the nest measured from the water surface to top of flower); (ii) distance of nest to water; (iii) water depth (mean of six samples at 2 m from the nest); (iv) number of horizontal (i.e. bent) reeds up to 20 cm above the nest; (v) the ratio of the surface areas of water to reedbed surrounding the nest within a radius of 5 m, given as a percentage (this variable is important for predator access and was shown to be relevant for fledging success in other reed-nesting passerines; Baldi & Kisbenedek 1999); (vi) the number of seed pods at 1 m^2 around the nest (index of reed productivity); and (vii) an index of nest concealment from 1 to 3, where 1 = exposed (>67 % nest visibility), 2 = covered (33–66 % nest visibility), 3 = well-covered (<32 % nest visibility).

Nest concealment as described above was assessed using the percentage of reed cover for three vantage points: (i) from below (at the water surface), (ii) the side (at nest level), and (iii) from above (20 cm above the nest). These variables were measured at 20 moustached warbler and 20 reed warbler nests at which we also performed the predator placements. In both species, nest concealment from below and the side were correlated (moustached warbler: $r = 0.76$, P < 0.001; reed warbler: $r = 0.78$, P < 0.001). Therefore, only nest concealment from below and nest concealment from above were used when examining the statistical relation between nest defence and nest concealment. All nest measurements were carried out once nests were terminated (either successfully or unsuccessfully) to minimise the impact of measurement on nest conspicuousness, and to reduce our activity at the nests prior to the experiment. All nests were accessed on foot via the waterways and never involved walking through reed beds, thereby causing no damage to vegetation surrounding the nest site.

Predator tests

Nest defence behaviour was recorded for three different predator types placed at the nest during the late feeding phase (chick age day 5–10): a grey/green plastic snake (25 cm long), a stuffed stoat, and a stuffed marsh har-

rier. Based on methodological reviews by Redondo (1989) and Weatherhead (1989), this was considered a reasonable research technique to examine nest defence responses for different predator types. The stuffed stoat was in normal walking position and was mounted on a wooden board. The stuffed harrier was in flight position, with extended wings, and was mounted on a bamboo pole.

Placement of the predators at the nest differed according to predator type. The snake and stoat were placed at water level 1 m from the nest, whereas the harrier was placed at 1 m above water level 1 m in front of, or above the nest. We selected the 1 m distance because observations of predators near nests during previous years showed that parent birds did not flush from the nest to harriers, stoats, snakes, rats or mice when these were farther away than 1 m (see also Burhans & Thompson 2001). Other observations of moustached warblers and reed warblers also showed that nest defence levels to the stoat and snake were higher at 1 m v. 5 m from the nest, with no difference to the harrier (S. Kleindorfer et al. unpubl.).

Tests lasted 5 minutes. Following the placement of the predator at the nest, the observer hid behind a mobile hide and recorded the following reactions every 10 seconds: adult alarm calls (total frequency irrespective of sex), latency of approach (the time in seconds until a bird was seen or heard at <5 m from the nest), and the distance from the predator. For the analyses, the minimum approach distance was used as a measure of risk taking. Predator placement varied randomly across nests on different days. Most nests were tested with each predator type, with the exception of nests taken by predators between experimental trials (moustached warbler: 4 nests taken between trials; reed warbler: 6 nests taken).

Statistical analyses

For each predator placement, we calculated a factor score of parental defence reaction using a Varimax rotated R-type orthogonal principal component analysis (PCA; Backhaus et al. 1990). The variables used were number of alarm calls, latency of approach to within 5 m, and minimum approach distance. This gave one single factor (hereafter referred to as reaction score) that significantly explained the different measures for parental defence accounting for 60.6 % of the variance
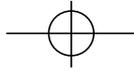
Table 1. The parental defence factor and accompanying factor scores extracted from an R-type orthogonal principal component analysis employing three measures of parental defence.

Parental defence Variable	Parental defence factor score
Alarm calls	0.67
Latency to approach (<5 m)	−0.85
Approach (minimum distance)	−0.8

(Table 1). High positive scores for alarm calls and high negative scores for latency of approach and minimum approach distance suggest that this new variable reflects an increase in alarm calls combined with a quicker and closer approach to the predator. Hence higher reaction scores imply higher risk-taking. We limited the analyses to these reaction scores to prevent a bias in specific components of the nest defence tactic (e.g. alarm calls: to whom are they directed? – see Kleindorfer et al. 1996). We did not discriminate between adult sex because there was a high degree of uncertainty when birds remained at a distance from the predator hidden in the reeds.

Parametric tests were used when assumptions for normality were met. Means ± s.e. are given throughout. The reaction scores were normally distributed. We used stepwise discriminant function analysis to examine nest site characteristics as discriminating variables for nest site across species and for predation outcome within species. To examine nest defence level in relation to nest concealment and predator type, we used a two-way ANOVA with adult nest defence level (using the reaction scores) as the dependent variable, and experimental placement of three different predator types (snake, stoat and harrier) and nest concealment (exposed, covered, well-covered) as the independent factors.

Results

Nest site characteristics

Nest height was significantly lower in the moustached warbler (35.5 cm ± 2.7) than in the reed warbler (85.3 cm ± 5.1; t-test: $t_{20,20} = 8.6$, $P < 0.001$). Only one nest site habitat variable, the number of bent reeds, entered

a stepwise discriminant function analysis (Wilks $\lambda = 0.84$, $F_{1,38} = 7.5$, $P < 0.009$) after a univariate F-test at a significance level of $P < 0.05$, explaining 100 % of the variance. Probably just as a consequence of the different nest height between species, the number of bent reeds above the nest was higher in moustached warblers (20.35 ± 3.3) than reed warblers (10.3 ± 1.7). Otherwise, there were no differences in any of the measured nest site characteristics.

Nest site characteristics and the probability of predation

Predation rates calculated for the nestling phase did not differ between moustached warblers (7/20 = 35 % of nests taken by predators) and reed warblers (8/20 = 40 % of nests; binomial test: $z = –0.3$, $P > 0.7$). In both species nest heights did not differ between those taken by predators (moustached warbler: 35.7 cm ± 3.1, n = 7; reed warbler: 87.5 cm ± 7.4, n = 8) and successful nests (moustached warbler: 35.4 cm ± 3.9, n = 13; reed warbler: 83.7 cm ± 7.2, n = 12; t-test: moustached warbler: $t_{13,7} = –0.6$, $P > 0.8$; reed warbler: $t_{12,8} = –0.3$, $P > 0.7$). Using a stepwise discriminant function analysis, we entered predation status (predated/successful) as the group variable and all vegetation parameters measured as well as nest concealment scores as the predictor variables. In the moustached warbler, only nest concealment from below entered the analysis (Wilks $\lambda = 0.75$, $F_{1,18} = 5.9$, $P = 0.026$). With this variable 80 % of all moustached warbler nests were correctly classified as taken by predators or successful. In the reed warbler, no vegetation parameters measured entered the analysis. Hence no habitat variable predicted predation events with the available sample size.

Nest concealment, predator type and nest defence

Using ANOVA, we examined adult nest defence level (using reaction scores) to the experimental placement of the three different predator types. The independent variables entered were (i) nest concealment (exposed, covered, well-covered) from below; (ii) nest concealment (exposed, covered, well-covered) from above; and (iii) predator type (snake, stoat and harrier). In the moustached warbler, reaction scores differed based on nest concealment from above, and almost reached sig-
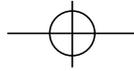
Table 2. Level of nest defence of parent moustached warblers and reed warblers in relation to nest concealment and predator type (ANOVA results showing F-values and P-values). The independent factors entered in the ANOVA were (i) nest visibility (exposed, covered, well-covered) from below; (ii) nest visibility (exposed, covered, well-covered) from above; and (iii) predator type (snake, stoat and harrier). The dependent variable was entered as the reaction score of the adult birds to experimental placement of the different predator types at the nest.

Species/Factors	F	P
Moustached warbler		
Predator type (A)	0.72	n.s.
Visibility below (B)	2.89	$P = 0.07$
Visibility above (C)	7.14	$P < 0.005$
Interaction (AB)	3.57	$P < 0.02$
Interaction (AC)	1.28	n.s.
Interaction (ABC)	0.85	n.s.
Reed warbler		
Predator type (A)	0.26	n.s.
Visibility below (B)	2.51	n.s.
Visibility above (C)	1.57	n.s.
Interaction (AB)	2.66	$P = 0.05$
Interaction (AC)	3.49	$P < 0.02$
Interaction (ABC)	0.09	n.s.

nificance for nest concealment from below (Table 2). We also found a significant interaction between nest concealment from below and predator type (Table 2), indicating the occurrence of predator-specific tactics for nest defence at different levels of nest concealment. Figure 1 shows that nest defence decreased with increasing nest cover from below against snakes, but we found no consistent pattern in defence against the stoat or harrier. Nest defence in relation to visibility from above showed an obvious decrease in the reaction against stoat, and the same tendency for snake but no real adjustment in reaction against the harrier.

In the reed warbler, there was a significant interaction between nest concealment from above and below and predator type (Table 2). Regarding nest concealment from below, this result is mainly due to decreasing nest defence against the snake and stoat at well-covered nests, with no change in reaction to the harrier (Fig. 2). Regarding nest concealment from above, reaction scores hardly differed between predator types (Fig. 2).

Nest defence and fledging success

To examine the percentage of chicks that fledged per nest in relation to mean nest defence level, we averaged reaction scores to snake, stoat and harrier per nest. In the moustached warbler, mean nest defence was positively related to the number of chicks fledged ($r = 0.72$, $P < 0.005$, $t = 3.8$). In the reed warbler, the level of nest defence was not related to fledging success.
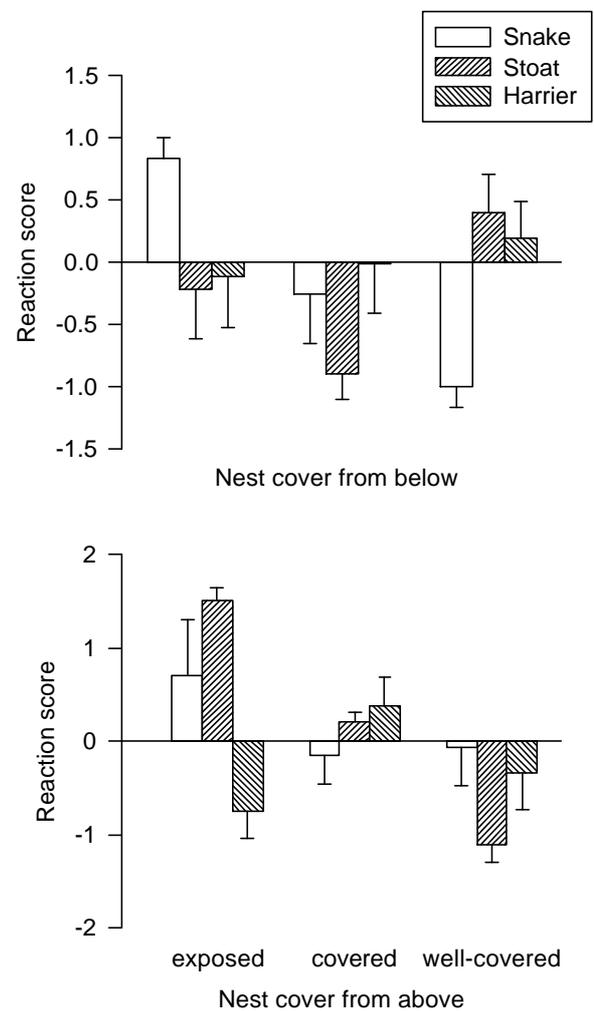
Figure 1. Predator-specific nest defence reaction scores of moustached warblers to different levels of nest concealment (exposed, covered, well-covered). The upper graph shows levels of nest defence against experimentally placed predators for nest concealment from below ($n = 9, 5, 6$), the lower graph for nest concealment from above ($n = 3, 11, 6$). Shown are means ± s.e. of the reaction scores (see Methods).
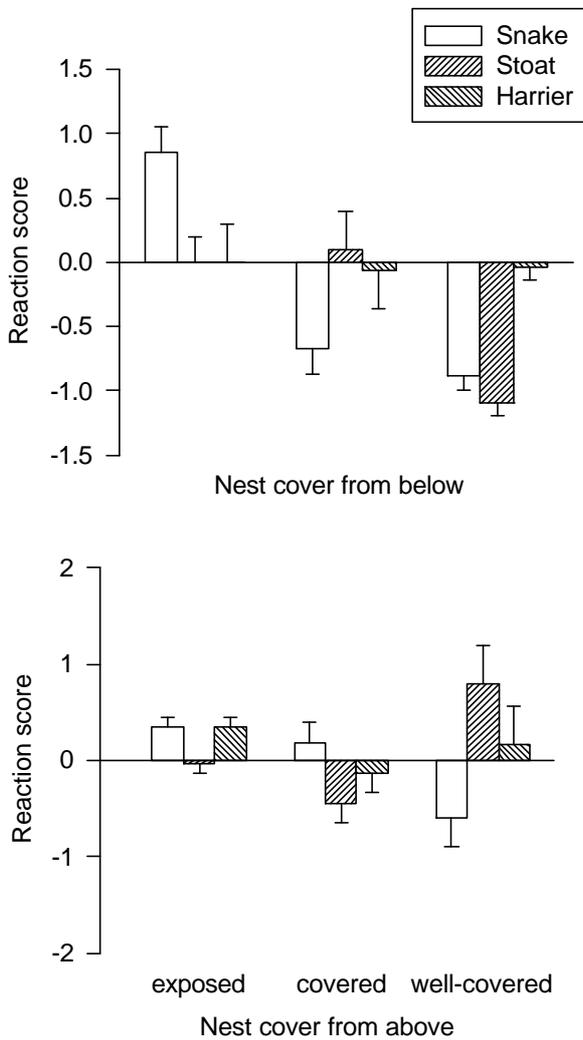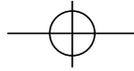
Figure 2. Predator-specific nest defence reaction scores of reed warblers to different levels of nest concealment (exposed, covered, well-covered). The upper graph shows nest defence against experimentally placed predators for nest concealment from below ($n = 9, 9, 2$), the lower graph for nest concealment from above ($n = 2, 11, 7$). Shown are means ± s.e. of the reaction scores (see Methods).

Nest defence during experiments was significantly higher for moustached warbler nests that finally fledged compared to nests that were taken by predators (Fig. 3; t-test: $t_{20,20} = 4.6$, $P < 0.01$). This was not the case in the reed warbler although the trend was in the same direction.

Discussion

The basis for predictions of the nest exposure hypothesis is that the relative risk of being taken by a predator is related to both predator type and nest visibility, i.e. that snakes and stoats are more likely predators for low-lying nests exposed from below, whereas harriers are more likely predators for high-lying nests exposed from above. The results of this study provide partial support for the nest exposure hypothesis in that parent moustached and reed warblers showed variable nest defence behaviour in relation to nest concealment and predator type. In both species, nest defence level was higher to snakes at nests exposed from below (Fig. 1 and 2), whereas there was no obvious change in defence behaviour to the stoat or harrier. For nest exposure from above, the pattern is less clear. In moustached warblers, nest defence was higher to the snake and stoat at exposed nests. In reed warblers, reaction scores hardly differed between predator types. In general, little variation in nest defence was observed in either species towards the harrier at nests exposed from below or above. Halupka (1999) also found evidence of predator-specific nest defence in the aquatic warbler, *Acrocephalus paludicola*, with higher nest defence to an experimentally placed polecat and lower nest defence to an experimentally placed harrier.
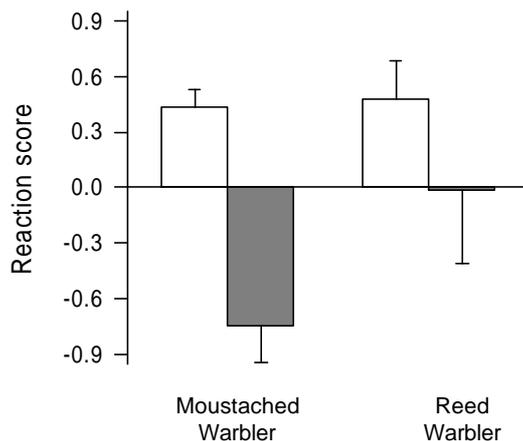
Figure 3. Nest defence levels at successful nests (hollow bars: moustached warbler = 13, reed warbler = 12) and those that were lost to predators (hatched bars: moustached warbler = 7, reed warbler = 8) during the period of nestling feeding. Nest defence is calculated as the average nest defence factor score for snake, stoat, and harrier (see Methods). Shown are means ± s.e.
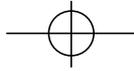
In moustached warblers, high nest concealment from below was significantly related to lower predation. In this species, adults showed higher nest defence to specific predators (snake and stoat) in relation to nest concealment, but not to the harrier. Finally, nest defence level was related to fledging success and suggests that parent birds may influence predation outcomes through behavioural tactics dependent on different levels of nest concealment. Due to the need/preference of moustached warblers for areas with bent reeds, suitable nest sites may be limited, more so than in reed warblers, and nest site may be an important criterion for female choice (B. Fessl & H. Hoi unpubl.).

Nest concealment in reed warblers, as measured in this study, was not related to predation outcome (see also Ille et al. 1996). Other studies on reed warblers carried out in the Czech Republic, Denmark and France have examined vegetation features around the nest (but not nest concealment) in relation to predation outcome and found a negative relationship between reed density and predation risk (Graveland 1997, Honza et al. 1998, Poulin et al. 2000, Prochazka 2000). This pattern was also found in the African reed warbler *A. baeticatus*, where nests in the tallest and densest reed patches suffered less predation (Eising et al. 2001). In a review of the ecology of predation in reed warblers by Schulze-Hagen et al. (1996), the authors showed that differences in nest concealment were associated with differential reproductive success in open-nesting and ecologically similar species pairs. Specifically, reed warbler nests were less concealed compared with nests of marsh warblers *A. palustris*, and more reed warbler nests were taken by predators compared with marsh warbler nests (Schulze-Hagen et al. 1996). Reed warblers must contend not only with predators but also brood parasitism by the common cuckoo *Cuculus canorus*. In a recent study, Clarke et al. (2001) found that nest exposure was the best predictor for cuckoo parasitism in reed warblers. Combined, these data suggest strong selection for adaptive nest site location in reed warblers. Small sample sizes in our study may explain why we did not find a relationship between nest concealment and predation events in reed warblers. An alternative explanation is that reed warblers showed behavioural compensation in relation to nest concealment, which overrode the unmodified effect of nest site characteristics for predation outcomes. We found evidence that nest defence in reed warblers varied as a function of the interaction between nest concealment and predator type, providing some support for this explanation.

We found a general overlap in breeding habitat characteristics between moustached warblers and reed warblers (Leisler 1991, Schulze-Hagen 1991, Hoi et al. 1995) but with two specific differences in nest site features. Moustached warblers built nests closer to water level than reed warblers (see also Leisler 1991, Schulze-Hagen 1991), and moustached warbler nests were covered by a higher number of bent reeds. This species-specific preference for different nest heights may explain the fitness consequences of nest site location and nest defence found in moustached warblers but not in reed warblers, if nest height is associated with different risk of predation or a different guild of predators. For example, the water-level location of moustached warbler nests may increase their susceptibility to detection by snakes or other water-based predators, whereas the mid-reed location of reed warbler nests (with less bent reed covering) may make them more susceptible to detection by terrestrial predators.

Vertical spacing of nests is predicted to lower predation risk by reducing the efficiency of predator search strategies (Hoi & Winkler 1988, 1994; Martin 1993a, 1998, Reitsma & Wheelan 2000). Previous research has shown predation rates to be dependent on prey density even if these varied in nest type (Martin 1988b,c, Hoi & Winkler 1994), and that vertical spacing of nests lowered prey density at typical prey sites (Martin 1993a,b, 1996). Thus, partitioning of nest heights among co-occurring species in response to nest predation is proposed to be an important process in the structure of avian species assemblages. Specific predators are often associated with different nest heights (Martin 1988b). Our study showed that both moustached warblers and reed warblers had higher nest defence responses to the snake and stoat, and responded only weakly to the experimentally placed harrier. When birds did respond to the harrier, they did so with alarm calls (and not mobbing) at a safe distance from the predator, and rarely approached the nest (S. Kleindorfer et al. unpubl., Halupka 1999). This different response intensity to the harrier could reflect a higher level of threat to the defending adult, thereby changing the cost-benefit ratio of parental care (McLean & Rhodes 1992). An alternative explanation is that low average nest placement in both moustached warblers and reed warblers, especially compared with the great reed warbler *A. arundinaceus*
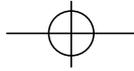
(unpublished data), made them less susceptible to harrier detection, but more vulnerable to snake and stoat detection.

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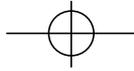
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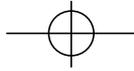
On the phylogenetic status of the British great tit
Parus major newtoni and blue tit
P. caeruleus obscurus

Laura Kvist

The phylogenetics of British great tits *Parus major newtoni* and blue tits *Parus caeruleus obscurus* were examined using mitochondrial DNA sequences. The analysis of molecular variance showed that 26 % of the variance in great tits and 35 % in blue tits was partitioned between populations when compared with their continental conspecifics. Phylogenetic trees showed that neither subspecies is monophyletic; instead, in both there are individuals that share the most common continental sequence. However, in both there are individuals that cluster together and separately from their continental counterparts. Classification of the British subspecies of the great and blue tit depends on the subspecies definition used.
Key words: great tit, blue tit, British subspecies, phylogeny, mitochondrial control region.

Department of Biology, POB 3000, FIN–90014 University of Oulu, Finland; email: laura.kvist@csc.fi

The use of molecular markers has revolutionised studies of phylogeny and phylogeography, and different kinds of markers are now also widely used in many fields of ecology. Many contradictory questions can be revisited and phylogenetic and phylogeographic problems are good examples of how molecular markers have become popular for enlightening old controversies. The subspecific rank of British great tits *Parus major newtoni* and blue tits *Parus caeruleus obscurus* are examples of such controversies.

The British Isles were mostly covered by ice during the last glacial maximum about 18 000 years ago, and the southern ice-free regions were covered by polar desert. At that time, the British Isles were still connected to continental Europe by a land bridge, which was broken due to the rise of the sea level by the Mid Holocene, c. 5000 B.P. During the maximum glaciation the flora and fauna of Britain was scarce, and no species requiring temperate conditions existed there. When the temperature rose again, the islands were recolonised, mainly from two southern European refuges. One recolonisation route led from the Iberian Peninsula, and the other, possibly the most commonly used, from the Balkans (Hewitt 2000). Many species found in Britain today have been classified as subspecies, differing in some characters from their continental counterparts.

The type description of the British subspecies of the great tit *P. m. newtoni*, was given by Prazak (1894). He reported that the British great tit is smaller and has duller plumage than the continental bird, characters that have later been questioned. Hartert (1907) first showed that the bill of the British great tit is stouter and more powerful than that of continental birds, and it was later agreed that the bill is the only character differing between continental and insular birds (see refs in Gosler 1999). Gosler (1999) re-examined the bill characters taking seasonal variation into account, and inferred that there are differences between the continental and British populations. However, with the bill being the only character differentiating the two, Gosler questioned the validity of the British *P. m. newtoni* as a recognised subspecies.

Prazak (1894) also gave the type description for the British blue tit, *P. c. obscurus.* He noted that the plumage of the insular birds is darker than that of the continental birds, and the British birds are also smaller. He noticed that British birds and Spanish birds are very
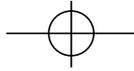
alike, even though the coloration of the Spanish birds is cleaner and more intensive (see also Harrap & Quinn 1996 and references therein). Based on these characters, he proposed that the British birds be recognised as subspecifically distinct. Later, Clancey (1947) stated that *P. c. obscurus* is a constant race throughout its range in England and Wales apart from paler and brighter birds in southeast England and the Salisbury Plain.

In this study, I have examined the phylogenetic status of British blue and great tits by sequencing part of the mitochondrial control region. Mitochondrial DNA is a small (approximately 16 kb in birds) circular molecule, which is maternally inherited in animals (but for exceptions see Kondo et al. 1990, Gyllensten et al. 1991, Zouros et al. 1992, Kvist et al. 2003). It does not recombine (but see Eyre-Walker et al. 1999, Hagelberg et al. 1999) and individuals are usually homoplasmic for one mitochondrial haplotype. The mitochondrial control region is the only non-coding part of the mitochondrial DNA; its function is to control the replication and transcription of the mtDNA. It usually evolves faster than the rest of the mtDNA, which, in turn, evolves about ten times faster than nuclear DNA. These features make the control region a good tool for studies concerning intraspecific relationships.

Materials and methods

Feathers were obtained from 7 blue and 10 great tits originating from the Loch Lomond field station, north of Glasgow, UK. The DNA was isolated by cutting the tips of the feathers into 100 µl of buffer containing 0.1 M Tris-HCl (pH 8.5), 0.5 mM EDTA, 0.2 % SDS, 0.2 M NaCl and 0.03 mg of proteinase K. The tips were incubated for 3 h at 56 °C and centrifuged for 10 min at 10 000 rpm after which the DNA was precipitated from the supernatant by 200 µl of ice-cold ethanol and 10 µl of 3M Na-acetate (pH 5.2), washed and diluted into 100 µl of sterile water.

A polymerase chain reaction (PCR) was performed with primers L16 700 and H590 for the great tit and L16 700 and H522 for the blue tit (Kvist et al. 1999a). PCR reactions were performed in 50 µl volume containing 5 µl of template DNA, 1.0 µM of each primer, 0.2 mM of each dNTP, 5 µl of 10 x PCR buffer (2.5 mM MgCl$_2$) and 1.0 unit of Dynazyme (Finnzymes). The amplification profile was 94 °C for 5 min followed by

35 cycles of 94 °C for 1 min, 53 °C for 1 min and 72 °C for 1 min and a final extension in 72 °C for 5 min. Sequencing reactions were performed with the primers H590 or H522 with a Big Dye TM Terminator Cycle Sequencing Kit v. 2.0 and run with an ABI 377 automatic sequencer.

The DNA sequences obtained were aligned with sequences from previous studies of European great and blue tits (Kvist et al. 1999a, 1999b). Two randomly chosen sequences were picked from each population for the alignments, except for a blue tit population from Barcelona, Spain, for which five sequences were included (because of the existence of two mitochondrial lineages, *P. c. caeruleus* and *P. c. ogliastrae* there). The sequences are deposited in GenBank under accession numbers AY136797-813. The analyses of molecular variance were performed with Arlequin v. 2.0 (with Tajima-Nei distances and haplotype frequencies, Excoffier et al. 1992), as well as estimation of nucleotide diversities (π, Nei 1987, eq. 10.6) and construction of minimum spanning trees. In addition, maximum likelihood (fastDNAml with 100 bootstraps, transition-transversion ratio for the blue tits 13.9 and for the great tit 4.5 and empirical base frequencies; Olsen et al. 1994) and neighbour-joining trees (1000 bootstraps and Tajima-Nei distance; Saitou & Nei 1987) were constructed. The phylogenetic program packages PHYLIP (v. 3.6; Felsenstein 2000) and FastDNAml (Olsen et al. 1994) were used for the analyses.

Results and discussion

The analysis of molecular variance showed that most of the variance of both great and blue tits was partitioned within populations compared with the continental subspecies. However, 26 % of the variance in great tits and 35 % in blue tits was partitioned between populations. The genetically effective number of migrants (Nm) between continental and British populations was estimated to be 1.36 per generation for great tits and 0.923 for blue tits. Nucleotide diversity for *P. m. newtoni* was 0. 0030 and for *P. c. obscurus* 0.0056, both values being larger than estimates from continental populations (0.0019 for both *P. m. major* and *P. c. caeruleus*; Kvist et al. 1999a,b).

The minimum spanning trees with bootstrap values from maximum likelihood and neighbour-joining me-

thods are shown in Figure 1. Neither British subspecies is monophyletic; in both great tits and blue tits there are individuals that are identical to the most common continental haplotype. However, in both there are clusters of individuals that differ markedly from the continental haplotypes. Six of the ten analysed *P. m. newtoni* form a common branch (with bootstrap support of 65 % by both phylogenetic methods) . Five of the seven *P. c. obscurus* (and one Spanish) birds form a common branch by the maximum likelihood method (bootstrap support 46 %), but the neighbour-joining method divides this branch further in two (bootstrap support 48 % for both branches).
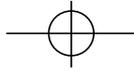
These results suggest that both subspecies of the great and blue tit have differentiated from the continental nominate conspecifics to some degree. However, migration, recolonisation history or incomplete lineage sorting may have confounded the discrimination from the nominate race by the method used here. Including samples from other British locations or sequencing a longer DNA region could provide further insight into this question.

Mayr (1963) defined the subspecies as 'a geographically defined aggregate of local populations which differ taxonomically from other subdivisions of the species'. The problem with definitions is to justify the

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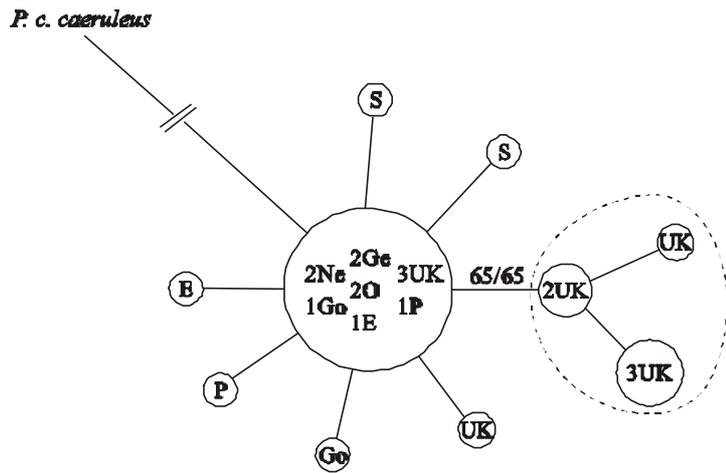
b. The blue tit

Figure 1. Minimum spanning trees of (a) great tits and (b) blue tits. The tree for the great tit is rooted with the blue tit and vice versa. Circles refer to haplotypes and bars to one substitution in the DNA sequence. S = Barcelona, Spain, Ge = Tübingen, Germany, E = Tartu, Estonia, P = Portugal, O = Oulu, Finland, Go = Gotland, Sweden, Ne = Hoge Veluwe, the Netherlands, U = Uppsala, Sweden, N = Oslo, Norway. Numbers on the branches represent the bootstrap support of the branch obtained by maximum likelihood and neighbour-joining methods, respectively (except for the one branch marked with n.d. bootstrap support could not be obtained by the neighbour-joining method; see text).
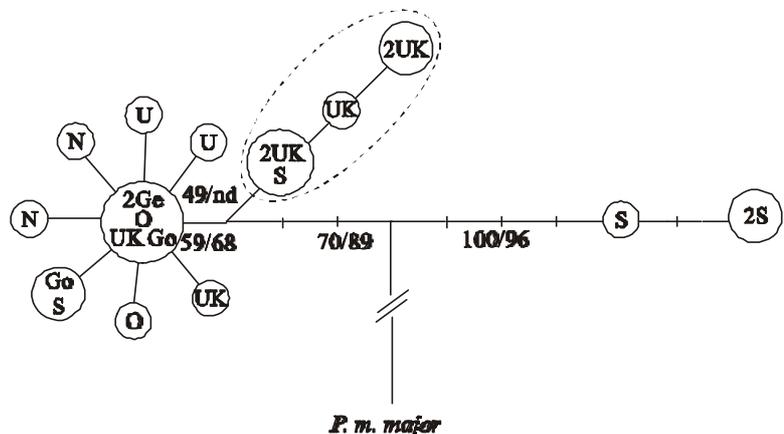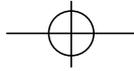
taxonomic differences. Perfect discrimination between populations, subspecies or species is impossible because traits change continually from one to another. O'Brien and Mayr (1991) tried to specify a subspecies as individuals that share a unique geographic range or habitat, a group of phylogenetically concordant phenotypic characters that can be described and a unique natural history relative to other subdivisions of the species. With regard to the British *P. m. newtoni* and *P. c. obscurus*, this subspecies definition certainly fits. The British birds do share a unique geographical range, there are several phenotypic characters that differentiate them from the continental birds (even though they are overlapping) and the colonisation history of the birds in the British Isles, followed by at least a partial isolation from their continental counterparts, give them a unique natural history compared to the continental birds. Ball and Avise (1992) suggested a more genetic approach for subspecies definition by arguing that 'subspecies names should be reserved for the major subdivisions of the gene pool diversity within species, best indicated by concordant subdivisions at multiple independent loci'. If this definition is applied, the British great and blue tits would not be considered to be subspecies. Even though the results suggest that the British birds are evolving in their own direction, there are not (yet) distinct subdivisions of the gene pool diversity because some birds share the identical haplotypes with the continental birds.

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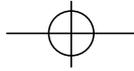
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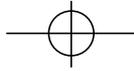
Nestling energy expenditure of Eurasian kestrels *Falco tinnunculus* in relation to food intake and hatching order

Sylvie Massemin[1]*, Erkki Korpimäki[1], Thierry Zorn[2], Ville Pöyri[1] and John R. Speakman[3]

In altricial birds asynchronous hatching of the nestlings may allow the first chick to monopolise food, ultimately ensuring that at least some young survive (the 'food amount hypothesis'). Asynchrony may reduce total nestling energy demands by reducing sibling rivalry (the 'sibling rivalry reduction hypothesis'). Energy demands may also be reduced because of the body size differences between hatchlings in asynchronous broods (the 'peak load reduction hypothesis'). We measured food delivery rates of adult Eurasian kestrels *Falco tinnunculus* and quantified the levels of sibling competition within broods by measuring nestling resting metabolic rates (RMR) and daily energy expenditures (DEE). DEE, measured using doubly-labelled water, was determined in first- and last-hatched nestlings (17 and 14 days old, respectively) from asynchronous broods that had been either food supplemented or not. Without food supplementation, DEE of the first-hatched nestling was 35 % higher than the last-hatched nestling, indicating that substantial competition was occurring. However, when asynchronous broods were provided with a food supplement, DEE declined and the difference in DEE between the first-hatched nestling and the last-hatched nestling disappeared. This indicates reduced sibling competition when broods were food-supplemented, thus supporting the 'food amount hypothesis'. DEE did not differ between the first-hatched nestling in asynchronous broods and a size-matched nestling from synchronous broods, suggesting similar levels of energy expended by the largest individual on sibling competition. However, the energy expended in competition by the smallest chicks was very low, resulting in a lower total brood energy requirements and parental food delivery rates of the adults in asynchronous compared to synchronous broods (13 % and 18 % respectively). Most (90 %) of this effect was due to the lower levels of activity of the smaller nestlings in asynchronous broods, providing some support for the 'sibling rivalry reduction hypothesis'. 10 % of this effect was due to differences in RMR because of the differences in nestling size, therefore supporting the 'peak load reduction hypothesis'.

Key words: Raptor, sibling competition, hatching asynchrony, doubly labelled water.

[1]Section of Ecology, Department of Biology, University of Turku, FIN–20540 Turku, Finland; [2]Office National de la Chasse, 17 Avenue de Wagram, F–75017 Paris, France; [3]School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, United Kingdom. *Corresponding author: S. Massemin, CNRS, CEPE, UPR 9010, associated with Louis Pasteur University, 23 rue Becquerel, F–67087 Strasbourg, France; email: sylvie.massemin@c-strasbourg.fr

The longevity and future reproductive prospects of avian parents are considered to be affected by their current reproductive effort. One measure of reproductive effort is the daily energy expenditure (DEE) of the adults, which depends mostly on their food provision rates (Drent & Daan 1980, Masman et al. 1989,
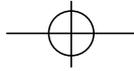
Slagsvold et al. 1995, Deerenberg et al. 1995, Daan et al. 1996). Survival and body condition of nestlings are related to both the parental provisioning rate and to their own energy expenditure. Part of the nestling daily energy expenditure results from sibling competition for food delivered to the nest by the parents. The intensity of this competition may depend on prey delivery rates and whether the young hatch synchronously or asynchronously. Hatching asynchrony, i.e. a hatching interval of more than one day, results in differences of age and size between nestlings. Older and larger nestlings usually out-compete younger ones for food, thus attaining higher body masses and higher survival rates (O'-Connor 1978, Zach 1982, Mock 1984).

Of the several hypotheses advanced to explain the fitness relevance of hatching asynchrony, the 'brood reduction hypothesis' contends that when food falls short, the first-hatched nestling will grow under optimal conditions while the last-hatched nestling is eliminated, thereby ensuring a greater fledging success in asynchronous than synchronous broods (Lack 1954). Although the brood reduction hypothesis has been tested and confirmed by many studies, some studies have failed to find strong support for it (e.g. Amundsen & Stokland 1988, Magrath 1990, Amundsen & Slagsvold 1991, 1996, Forbes 1994, Wiehn et al. 2000), suggesting that other factors may also be important. Several additional advantages have been postulated for asynchronous over synchronous broods.

Peak load

Food requirements of nestlings depend on their size. Because the food requirements of individual nestlings in asynchronous broods peak at different times the total demands and thereby the amount of food the parents must provide on any given day are reduced during the nestling period compared to synchronously hatched broods – the 'peak load reduction hypothesis' (Hussell 1972, Mock & Schwagmeyer 1990).

Sibling rivalry

Different sizes of siblings may facilitate the development of a stable dominance hierarchy. Consequently, young in asynchronous broods may compete less intensively for food, therefore wasting less energy in fighting compared to synchronous broods (Hahn 1981) – the 'sibling rivalry reduction hypothesis'. This effect might further reduce the peak energy requirements of the brood.

Food abundance

In addition to the effect of the size-hierarchy it is also clear that food abundance also affects sibling competition. The first-hatched and therefore dominant nestlings might usurp a greater proportion of food when food availability is low, but when food delivery rates are high the competition may disappear – the 'food amount hypothesis' (Mock et al. 1987). This hypothesis has been supported by studies showing that the first-hatched nestling in asynchronous broods dominates access to food by either winning fights (Mock & Ploger 1987) or passively dominating younger siblings (Forbes 1991).

These hypotheses are not mutually exclusive. For example, the primary outcome of sibling rivalry reduction will be a reduction in offspring food demands, thereby contributing to reduction in the peak load. Moreover, externally imposed reductions in food delivery rates (food amount) may stimulate sibling rivalry independently of whether there is also a reduction in peak load, or less sibling rivalry in asynchronous compared to synchronous broods.

Most previous work on the relevance of hatching asynchrony for reproductive success has been focused on the growth and survival of nestlings (Nilsson & Svensson 1996, Royle & Hamer 1998). While this body of work provides estimates of the direct effects of asynchrony on parameters relevant to fitness, the underlying energetic mechanisms remain obscure. Here we assess the importance of the 'peak load reduction', 'sibling rivalry reduction' and 'food amount' hypotheses for the Eurasian kestrel *Falco tinnunculus*. We evaluated the 'food amount hypothesis' by quantifying the energy expended by chicks in scrambling competition as a function of daily food intake. We anticipated that the difference between resting and daily energy expenditure would primarily reflect the activity of the nestlings, which in large part depends on the energy expended during scrambling competition. We predicted that if food amount was a factor influencing the level of competition then by providing food supplements we would reduce the overall level of competition and in turn the difference between the DEE and resting metabolic rate (RMR) of the nestlings. We evaluated the 'peak load reduction hypothesis' by measuring the food delivery rates of parent birds to asynchronous and synchronous nests. We anticipated that if the peak load was reduced in asynchronous broods food delivery rates would also be lower. Finally we evaluated the contri-

bution that development of a stable hierarchy might have on nestling energy demands by comparing the difference between DEE and RMR of first-hatched offspring from asynchronous broods with that of individuals of the same size from synchronous broods. Because of the development of a stable hierarchy the 'sibling rivalry reduction hypothesis' predicts that the energy demands of the individual in the asynchronous brood would be lower than those of the same-sized individual in the synchronous brood, primarily due to a reduction in energy allocated to activity (competition).
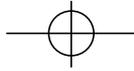
Material and methods

Study area and species

The study was conducted in 1998 in South-Ostrobothnia, western Finland (63°N, 23°E). The main study area consisted of flat agricultural land broken by small islands of trees, bushes and woods. In this open agricultural landscape, kestrels breed in nest-boxes mounted on barns and solitary trees.

The main food of kestrels in the area is voles (Korpimäki 1985, 1986), whose density fluctuates in 3–4-year cycle with an amplitude of up to 100-fold within a cycle (Korpimäki & Norrdahl 1991). Compared to biannual (May and September) snap-trapping data from 1973–97 (Norrdahl & Korpimäki 1995), vole densities were very low in spring and summer 1998, which meant that food was scarce during the entire kestrel breeding season.

Because yearling males, which are easily identifiable in the field by their female-like plumage, rear smaller broods than adult males (Korpimäki & Wiehn 1998), we used only nests of pairs with adult males.

Several meteorological parameters were recorded. Nest temperature was obtained by using a Hobo data logger set to record temperature every minute during 24 hours.

Nestling parameters

The degree of asynchrony within kestrel broods ranged from nil (5 % of broods) to 10 days (1 %) but the majority (52 %) hatched within 2–3 days (267 nests over 12 years; Wiebe et al 1998). We randomly selected naturally asynchronous and synchronous nests in this population. Among asynchronous broods (n = 11), we

took all measurements of the first- and last-hatched chicks just after the brooding period. The first-hatched nestling was on average 16.9 ± 0.3 days old and the last-hatched nestling 14.0 ± 0.5 days. Among these asynchronous nests, six nests were provided with food supplements from hatching onwards and five remained unsupplemented. In addition, five naturally asynchronous broods without food supplements were compared to six naturally synchronous broods without food supplements. Because all nestlings in the synchronous broods were of similar body size, one chick was randomly chosen for the comparison with the asynchronous broods. The first-hatched chick of asynchronous broods and the chick randomly chosen in these synchronous broods were of similar age (17.4 ± 0.7 v. 16.3 ± 0.2 days, $t_9 = 1.63$, $P = 0.14$).

Mean hatching dates of nests without and with food supplements were similar among asynchronous broods (15 June $\pm$ 3 days v. 18 June $\pm$ 2 days, $t_9 = 1.27$, $P = 0.23$), as well as in asynchronous v. synchronous broods without food supplements (15 June $\pm$ 3 days v. 20 June $\pm$ 4 days, $t_9 = 1.12$, $P = 0.31$). There was no differences in brood size between nests without and with food supplements among asynchronous broods during the mid-nestling period (4.4 ± 0.2 v. 4.3 ± 0.3, $t_9 = 0.28$, $P = 0.88$), nor between asynchronous and synchronous broods without food supplements (4.4 ± 0.3 v. 4.2 ± 0.2, $t_9 = 0.81$, $P = 0.44$).

Three of the last-hatched nestlings died during the first 10 days of the nestling period in asynchronous broods (2 nestlings in broods without food-supplements and one in a brood with food supplements), so the second smallest chick was chosen to represent the last-hatched one. Thereafter, the fledging success calculated after 10 days was 100 % in asynchronous broods with food-supplements, 95 % in asynchronous brood without food-supplements, and 86 % in synchronous broods.

Wing length and the length of the sixth primary feather were measured to the nearest 1.0 mm; tibiotarsus and tarsometatarsus lengths were measured to the nearest 0.1 mm. The chicks were weighed to the nearest 1g using a spring balance. As an estimate of body size we used the first principal axis (PC1) resulting from principal component analysis of the measurements of wing, primary, tibiotarsus and tarsometatarsus, which explained 86 % of the total variance of body size of chicks in all nests (Rising & Somers 1989, Freeman & Jackson 1990). As a size-independent measure of chick
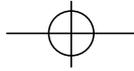
condition we used the residual of the regression of body mass on body size (PC1) (Hayes & Shonkwiler 2001).

Food supplementation and monitoring of prey deliveries

Dead domestic chicks *Gallus domesticus*, weighing about 30 g each, were provided inside the nestboxes to kestrel nestlings in supplemented broods throughout the nestling period (i.e. from when the first-hatched young was 1–2 days old to the time of fledging, when the last-hatched chick of the brood was 26 days old). Broods were fed with one domestic chick per nestling every two days during the first week after hatching, and thereafter with two domestic chicks per nestling every two days. This amount of food supplement corresponds to approximately half of the daily food requirement of kestrel nestlings (Masman et al. 1989). During the first two weeks of the nestling period, female kestrels fed the young and sometimes hid the remaining chicks on the ground in the vicinity of the nest for later use (Wiehn & Korpimäki 1997). By the end of the nestling period, young kestrels consumed these food-supplements by themselves. Male kestrels did not eat the food-supplements provided in nest-boxes.

The number of feeds was determined by video recordings (Panasonic WV-CP222 camera with WV-LA210C3 lens (2.1 mm, 1:1.0), Panasonic AG 6124 video recorder; see Wiehn et al. 2000). Twenty-four hours of continuous recording were carried out in three asynchronous and three synchronous broods simultaneously with the measurements of daily energy expenditure. Because parents sometimes perched for a few seconds in the entrance hole of the box without delivering prey, we included only visits with a prey item. We ignored the few visits with insect deliveries because the biomass of these items was negligible (<0.5 g, Korpimäki 1985). Food delivery rates were calculated by dividing the number of visits with food by the length of the daylight period.

Resting metabolism

Resting metabolism was evaluated by oxygen consumption of nestlings in the early morning after sunrise (after 03.00 hrs) but before the first meal. We used a portable oxygen analyser (Oxor II, Bacharach) that was connected to a darkened chamber (volume of 1768 cm^3)

in which chicks were placed. Organised as a closed circuit, air was pumped through the analyser and returned to the chamber gas, providing gas homogeneity in the system. To avoid hypercapnia, measurements were made within the range of decreased fractional oxygen concentration (ΔFo_2) between 20.9 % and 18.9 %. Three measurements taken at 1 minute intervals were averaged. Measurements were taken only when the nestling was at rest. Oxygen consumption was obtained by using the following formula: $n = \Delta PV/RT$, where n was the number of moles of oxygen per minute and ΔP was the partial pressure: $\Delta P = \Delta Fo_2 * (P_t - P_{H_2O})$, where P_t was the total pressure (760 mm Hg) and P_{H_2O} was the water-vapour pressure (for each value of box temperature) calculated by the theoretical relation between temperature and water-vapour pressure (Comroe 1966). V was the volume in which gas distribution is homogeneous: V was obtained by using the box volume minus the chick volume (estimated from the mass of the chick and body density of 0.90 g.cm^{-3}; Sturkie 1976) and the volume of the analyser's tubes. R was the universal gas constant (0.082 l.atm.K^{-1}.mol^{-1}), and T was the absolute temperature measured by a thermometer (K = 273 + T_{box} in Kelvin). Resting metabolism in kJ was calculated by using an energetic equivalent of 19.8 kJ per litre O_2 (Masman & Klaassen 1987).

Daily energy expenditure

Daily energy expenditure was measured using doubly-labelled water (DLW) (Lifson et al. 1955, Nagy 1980, Speakman 1997). Visser & Schekkermann (1999) showed that this technique can be used in growing birds if growth is less than 15 % of the mass per day (growth of kestrel nestlings was less than 7 % in our study). After weighing, nestlings were injected intraperitoneally with a mixture of stable isotopes H$_2^{18}$O (64 %) and D$_2^{16}$O (33 %). The injected volume of mixture ranged from 0.14 to 0.23 ml according to nestling body mass. After an equilibration time of 1 hour (see Speakman 1997 table 6.7), the initial blood samples were taken by puncturing the brachial vein. Blood samples were collected into three flame sealed 100 µl micro-pipettes. After 24 h, birds were weighed again and final blood samples were taken. Background measures of both ^{18}O and deuterium concentration were estimated from three individuals. Blood samples were distilled using the pipette method of Nagy (1983). Mass spectrometric
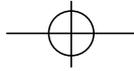
analysis of deuterium enrichment was performed using H_2 gas, produced from the water distilled after reaction with $LiAlH_4$ (Ward et al. 2000). For analysis of oxygen-18 enrichment, distilled water was equilibrated with CO_2 gas using the small sample equilibration technique (Speakman et al. 1990).

According to the validation of the DLW technique in growing shorebird chicks (Visser & Schekkermann 1999), we estimated CO_2 production using the single pool deuterium equation from Speakman (1997), assuming evaporative losses were 25 % of total water flux. The error in individual estimates was determined using the iterative procedures outlined in Speakman (1995). Conversion to energy expenditure was made using an assumed RQ of 0.8. All calculations were made using the Natureware DLW software (Speakman & Lemen 1999).

Statistical analysis

To test the 'food amount hypothesis', we used a repeated-measures ANOVA to test for the effects of hatching order (first- v. last-hatched nestlings in asynchronous broods) and the treatment (food supplement or not). We tested the other hypotheses on asynchrony using ANCOVAs to account for the effects of body mass. Type of brood (asynchronous v. synchronous) was the independent factor and body mass of nestlings was the co-

variate. Heterogeneity of regression slopes was tested by factor-covariate interaction. Comparisons of two means (± s.e.) were performed by Student's t-test or, when the assumption of normality failed, by Mann-Whitney U-test. Because data from chicks of a brood were not independent, the homogeneity of residual errors of all linear regressions included in this study was checked with the Kolmogorov-Smirnov test ($P > 0.05$). All statistical tests were performed using SPSS for Windows (Norusis 1993).

Results

Energy expenditure, hatching order and food-supplement

To test the 'food amount hypothesis' we compared RMR, DEE and the difference between RMR and DEE between the first- and last-hatched nestlings in asynchronous broods both with and without food-supplementation. Independent of food supplementation, body mass was 16 % larger in first-hatched than last-hatched nestlings in unsupplemented nests and 20 % larger in food supplemented nests (Table 1 and 2). This difference in mass was mirrored by a difference in structural size as revealed by the principal component scores (Table 2). These differences were to be expected

Table 1. Energetic and morphological parameters of first and last-hatched kestrel nestlings in asynchronous broods when supplemented by additional food or unsupplemented.

Variables	Without food			With food		
	n	Mean	s.d.	n	Mean	s.d.
First-hatched nestling						
Body mass	5	190.20	12.87	6	208.00	15.81
Body size	5	0.33	0.57	6	0.79	0.26
Body condition	5	−4.87	15.75	6	1.42	11.14
RMR (kJ.bird^{-1}.day^{-1})	5	153.84	17.77	6	173.89	22.99
DEE (kJ.bird^{-1}.day^{-1})	4	337.25	95.63	4	152.10	44.40
Last-hatched nestling						
Body mass	5	163.80	36.03	6	173.00	38.48
Body size	5	−0.99	1.12	6	−0.76	1.04
Body condition	5	2.30	26.68	6	5.68	13.29
RMR (kJ.bird^{-1}.day^{-1})	5	132.17	35.95	6	146.49	38.53
DEE (kJ.bird^{-1}.day^{-1})	4	220.01	63.50	4	246.39	132.44
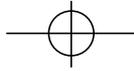
Table 2. ANOVA table for the effect of hatching order (first- and last-hatched nestlings) with repeated measures and of treatment (food supplement or control) on body mass, size and condition index of kestrel nestlings in naturally asynchronous broods.

Variables	Body mass			Body size			Body condition		
	df	F	P	df	F	P	df	F	P
Hatching order (H)	1	8.73	**0.016**	1	19.81	**0.002**	1	1.00	0.344
Treatment (T)	1	0.99	0.346	1	0.83	0.386	1	0.30	0.596
H × T	1	0.17	0.693	1	0.12	0.739	1	0.07	0.801
Error	9			9			9		

The present data meet the Sphericity assumption.

because of the different ages of the nestlings in asynchronous broods. The body condition index however did not differ significantly between the first and last-hatched nestlings (Table 2) suggesting that the smallest chick was not being disproportionately deprived of resources. Food supplementation and the interaction of food supplementation and hatching order had no significant effects on body size or condition index of chicks (Table 2).

Resting metabolism measured in the early morning was not correlated with air temperature outside the box ($R^2 = 0.01$, $P = 0.68$, $n = 29$). Resting metabolism was significantly higher in the first-hatched than in the last-hatched nestling independent of the food supplementation (Tables 1 and 3). On average RMR was 16 % higher in the first-hatched nestling in unsupplemented nests and 18.7 % higher in supplemented nests. Resting

metabolic rate was strongly correlated with body mass ($R^2 = 0.42$, $P < 0.0001$, $n = 29$) and the difference in RMR between the first- and last-hatched nestlings was very similar to the difference in their body masses (above). We removed the effect of body mass by fitting a least squares regression to the data for all chicks and calculating residuals to this regression. Residuals of resting metabolism did not differ significantly between the first and last-hatched nestlings (Table 3). This indicates that the differences in RMR were mainly due to the differences in body mass between first and last-hatched nestlings. Food supplemention and the interaction with supplementation and hatching order had no effect on resting metabolism or its residuals (Table 3).

Like RMR, daily energy expenditure was higher in the first-hatched than in the last-hatched chick (Tables 1 and 3, Fig. 1). However, in contrast to the variation

Table 3. ANOVA table for the effect of hatching order (first- v. last-hatched) with repeated measures and of treatment (food supplement or control) on resting metabolism and daily energy expenditure of kestrel nestlings in naturally asynchronous broods.

Variables	Resting metabolism					Daily energy expenditure		
	kJ.bird⁻¹.day⁻¹			kJ.day⁻¹*		kJ.bird⁻¹.day⁻¹		
	df	F	P	F	P	df	F	P
Hatching order (H)	1	6.39	**0.032**	0.20	0.668	1	10.54	**0.018**
Treatment (T)	1	2.44	0.153	1.37	0.273	1	6.23	**0.047**
H × T	1	0.34	0.573	0.84	0.384	1	20.03	**0.004**
Error	9					6		

The present data meet the Sphericity assumption.
*The effect of nestling body mass on resting metabolism and daily energy expenditure was removed and the residuals used in analyses.
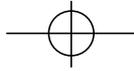
Figure 1. Daily energy expenditure (kJ.bird^{-1}day^{-1}) of first- and last-hatched kestrel nestlings in asynchronous control and food supplemented nests. Values with different labels are significantly different in control and food supplemented nests (ANOVA in Table 3, Tukey test, P < 0.05).
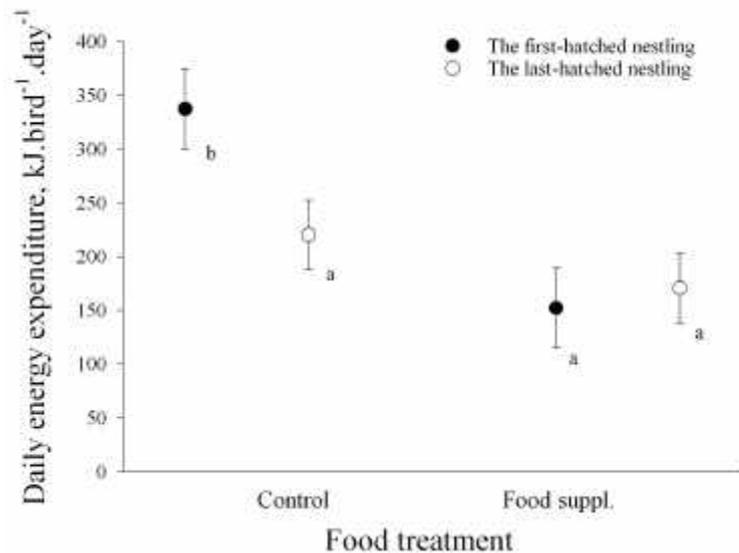
observed in RMR, both the food treatment and the interaction between food treatment and hatching order, significantly affected DEE (Tables 1 and 3). On average in the nests that received no supplementation DEE was 35 % higher in the first-hatched than the last-hatched chick compared with the 16 % difference in body mass and RMR. In food supplemented nests, however, a very different pattern emerged. Daily energy expenditure was considerably reduced in the first-hatched nestling, on average 55 % lower than the expenditure in unsupplemented nests. DEE of the last-hatched chick, however, was unaffected by the food supplementation treatment (Table 1, Fig. 1). Because of the large treatment effects on DEE there was no significant relationship between DEE and body mass when all the data were pooled ($R^2 = 0.02$, P = 0.56). Including body mass as a covariate in the analysis did not affect the significance of the hatching order, treatment or interaction effects.

The difference between RMR and DEE and the ratio of DEE to RMR provide estimates of the energy allocated to physical activity and thermoregulatory demands. Since the nest temperature was similar between control and food supplemented nests ($21.4 \pm 1.6 \,°C$ v. $18.1 \pm 1.5 \,°C$, $t_9 = 1.54$, P = 0.16), the effects on DEE-RMR and DEE/RMR reflect differences in physical activity. In unsupplemented nests the energy spent on physical activity (DEE-RMR) by the first-hatched nestling at 183 kJ/day was substantially greater than in the last-hatched nestling at 87 kJ/day. When additional

food was provided, however, the difference between DEE and RMR declined to –18 kJ (not significantly different from zero) in the first-hatched nestling but remained at around 100 kJ/day in the last-hatched nestling. The ratios of DEE/RMR were 2.19 and 1.66 in the first-hatched and last-hatched chicks respectively in unsupplemented nests, and these ratios altered to 0.87 and 1.68 when food supplements were provided. We conclude that there was a marked effect of supplementation on the metabolism of the first-hatched nestling, but no effect on the last-hatched nestling.

Energy expenditure and hatching asynchrony

We compared the same energetic variables between the first-hatched nestling of asynchronous broods and single nestlings chosen randomly from synchronous broods (Table 4). We found no significant differences between the two hatching strategies in chick body mass, condition index, resting metabolism and daily energy. The effect sizes were also small (less than 5 % in all cases) suggesting that the absence of any statistical significance was not a Type 2 error due to the low power associated with the relatively small sample size.

Using these data we estimated the total energy requirements for asynchronous and synchronous kestrel broods of four chicks. We used the measured energy demands of 337 and 220 kJ.bird^{-1}.day^{-1} for the first- and last-hatched chicks, respectively (see Table 1 and Fig.
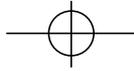
Table 4. Comparison of body mass, size, condition index, resting metabolic rate (RMR) and daily energy expenditure (DEE) between first-hatched kestrel nestlings from naturally asynchronous broods ($n = 5$) and single nestlings chosen randomly from naturally synchronous broods ($n = 6$). All nests were without food supplements.

Type of brood	Asynchronous broods	Synchronous broods	Test		
	Mean ± SE	Mean ± SE	Df	t	P
Body mass g	190.2 ± 5.8	195.0 ± 10.9	9	0.37	0.72
Body size	0.33 ± 0.26	0.53 ± 0.14	9	0.70	0.50
Body condition	4.87 ± 7.05	4.96 ± 7.70	9	0.01	0.99
RMR kJ.bird^{-1}.day^{-1}	153.8 ± 8.0	147.5 ± 7.5	9	0.58	0.57
DEE kJ.bird^{-1}.day^{-1}	337.3 ± 47.8	321.6 ± 34.5	7	0.27	0.79

1). We do not have direct measurements of the energy demands of the second- and third-hatched nestlings and therefore estimated these to be 279 kJ.day^{-1} (mean value of 337 and 220 kJ.day^{-1}). Because we had selected individuals at random for measurement in synchronous broods we used the average measured DEE of 322 kJ.day^{-1} for the estimated metabolism of all four chicks in synchronous broods. On this basis the total daily energy demands of the broods would be 1288 kJ.day^{-1} for synchronous broods and 1115 kJ.day^{-1} for asynchronous broods, a difference of 173 kJ.day^{-1} or a reduction of 13 % in asynchronous relative to synchronous broods. Using similar assumptions we estimate the energy spent on RMR would amount to 590 kJ.day^{-1} in synchronous broods and 572 kJ.day^{-1} in asynchronous broods, a difference of only 18 kJ.day^{-1} (3 %). Differences in resting metabolism due to differences in body mass in synchronous and asynchronous broods accounted for only about 10 % (18/173) of the difference in daily energy demands between these brood types.

Food delivery rates

The rate of food delivery was significantly lower in asynchronous than in synchronous broods (0.62 ± 0.05 versus 0.76 ± 0.02 prey items/hour, $U_{3,3} = 0$, $P = 0.05$). The food delivery rate of parents of asynchronous broods was thus reduced by 18 % compared to synchronous broods. This result agrees well with the estimates of the total energy demand of the two brood types.

Discussion

Hatching order

The present results show that, in asynchronous kestrel broods, body mass, body size, resting metabolic rate and daily energy expenditure were higher in the first-hatched nestlings compared to those in the last-hatched nestlings. The direction of these results is unsurprising given the age difference between the first and last-hatched chicks. The real significance of our data, however, comes from quantification of the effects. Body mass and resting metabolism were both elevated by around 16 % in the first-hatched chick and the absence of any effect of hatching order on residual RMR points to the difference in RMR being solely due to the body mass difference. In contrast the difference in DEE was substantially greater, with the first-hatched chick spending 35 % more energy than the last-hatched nestling. It is unlikely that this difference results from different thermoregulatory demands (as the chicks are in the same thermal environment) or simply from age differences (as the analysis accounted for body mass). Some of the difference might be attributed to the greater heat increment of feeding in the larger chick which is eating more food. We estimated that this effect might account for 4.5 % of the difference in energy expenditure between the first- and last-hatched nestlings (calculated from Trayhurn & James 1983). Therefore, a major part of the difference in DEE is probably attributed to nestling activity, especially competition for food. In Eurasian kestrels, a species in which direct aggression among sibling is rare, chicks jostle for a front position in the nest to be the first to intercept prey items from parents, as in the American kestrel *Falco sparverius*
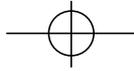
(Anderson et al. 1993). This dominance finally results in a higher body condition of the first-hatched nestling compared to the last-hatched nestling not at 17 days-old, but at the end of the nestling period (Massemin et al. 2002).

Food amount

Contrary to the results found in asynchronous control nests, the first- and last-hatched nestlings in asynchronous broods had similar daily energy expenditures when provided with a food supplement. This equality resulted from a decline in the energy expended on physical activity by the first-hatched nestling. The consequence was a reduction in total daily energy expenditure in food-supplemented compared with the unsupplemented control nests. We conclude from this that scrambling competition declined when food was supplemented. Our data suggest that energy expended in scrambling competition appears to be controlled proximately by the amount of food provided by the parent kestrels. These results therefore support the 'food amount hypothesis', which contends that sibling competition is temporally associated with food quantity when nestlings are presumed to be more hungry, and are in accordance with several studies performed in facultatively siblicidal species (Fujioka 1985a, Drummond & Garcia Chavelas 1989, Machmer & Ydenberg 1998).

We found that scrambling competition can account for up to half of the daily energy demands of kestrel nestlings (comparison of the first-hatched nestling between unsupplemented control and food supplemented nests, Table 2, Fig. 1). In this context, it would be important to distinguish between the energetic costs of chicks associated with scrambling and begging. According to the species, begging has been found to be either increased or reduced when a food supplement is given (Mock & Parker 1998). The study of begging in kestrel nestlings would provide more information about the parent-offspring conflict, particularly if parents control what they give to each of their young (begging model) or if they exercise any distributional control over the resources (scramble control, Mock & Parker 1998).

Benefits and costs of hatching asynchrony

Because we have shown that the first-hatched nestling spent more energy in scrambling competition than their last-hatched siblings in asynchronous broods, we compared the first-hatched nestling of asynchronous broods and one nestling of synchronous broods. The 'sibling rivalry reduction hypothesis' predicts a lower energy expenditure for the first-hatched nestling of asynchronous broods compared to individuals in competition with other nestlings of the same size (synchronous broods), because of the establishment of a stable dominance hierarchy that reduces the need for competition in asynchronous broods. Our data do not support this prediction because there was no difference in energy expenditure between these two kinds of nestlings. However, the energy allocated to scrambling competition by the last-hatched chick was much lower than the energy expended by the first-hatched nestling. Hence, in asynchronous broods the energy allocated to scrambling competition is substantially reduced overall. Indeed we estimate that approximately 90 % of the energy saving by asynchronous broods can be attributed to a low physical activity of the smaller nestlings, compared to only 10 % stemming from differences in RMR attributable to their smaller sizes. The saving of energy wasted in scrambling competition in asynchronous broods is the major contributor to the reduction in peak requirement of about 13 % compared to synchronous broods. The 13 % lower estimated energy expenditure of asynchronous broods matches the observed 18 % reduction in parental feeding rates in asynchronous broods relative to synchronous broods. This confirms earlier studies of kestrels (Wiehn et al. 2000) and other species (cattle egrets *Bubulcus ibis*: Fujioka 1985b, Mock & Ploger 1987; jackdaw *Corvus monedula*: Gibbons 1987; blue-footed booby *Sula nebouxii*: Osorno & Drummond 1995).

Our study provides some support for all of the proposed hypotheses – which are in any case not mutually exclusive explanations of the asynchronous hatching phenomenon. Experimentally manipulating food supply altered the amount of energy allocated to scrambling competition, particularly by the first-hatched nestling in asynchronous broods, supporting the prediction of the 'food amount hypothesis' that levels of competition should be responsive to food supply.

Total brood expenditure was lower in asynchronous compared with synchronous broods. One part of this difference (10 %) is attributable to the different nestling sizes in the asynchronous broods, which is consistent with the 'peak load reduction hypothesis'.
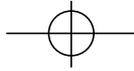
Moreover, the major part of the difference in expenditure (90 %) was a consequence of lower expenditure on competition by the smaller nestlings in the asynchronous broods, which is consistent with the 'sibling rivalry reduction hypothesis', although no saving resulted from reduced activity and aggression in the first-hatched nestling. Work on American kestrels also supports this hypothesis. Wiebe and Bortolotti (1994) found that the total preys provisioning by parents during all the nestling period were lower in asynchronous compared to synchronous broods, which is consistent with a reduced sibling rivalry in asynchronous broods.

Our study has demonstrated significant differences in the energetic mechanisms underlying the two hatching strategies. Asynchronous hatching may considerably reduce the peak energy demand of the brood. However, the adaptive significance of hatching asynchrony has to be considered at the level of both offspring and parental survival. Previous studies on the Eurasian kestrel in the same study area have shown a higher frequency of synchronous hatching when food is scarce but predictable (Wiebe et al. 1998), as well as higher fledging success and nestling body mass in synchronous broods (Wiehn et al. 2000). This indicates that the fitness consequences of both hatching strategies may vary locally and temporally depending on the between-year variance in environmental conditions.

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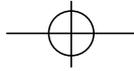
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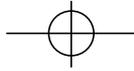
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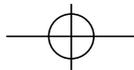
Migratory song thrushes *Turdus philomelos* hunted in Europe: survival rates and other demographic parameters

Vladimir A. Payevsky[1] **and Vadim G. Vysotsky**

Long-distance ringing recoveries of song thrushes ringed in the Eastern Baltic between 1957 and 1999 were analysed to determine the circumstances of recovery and annual survival rate. Of 358 recoveries, 86 % referred to birds killed by hunters and bird-catchers. The highest proportions of recoveries due to hunting were recorded in France, Italy, Spain, and Portugal (73–93 %), whereas in other countries only 28 % were recovered in this way. Survival probabilities of the song thrush estimated for different time periods varied between 0.368 and 0.420 for first-year birds and between 0.561 and 0.633 in adults. In the British Isles, where the song thrush is mainly a year-round resident and is not a quarry bird, adult survival rates did not differ from the values obtained for the Baltic populations, whereas first-year survival was somewhat higher than in Baltic birds.

Key words: Song thrush, *Turdus philomelos*, first-year survival rate, annual adult survival rate, age distribution, hunting bag.

Zoological Institute, Russian Academy of Sciences, 199034 St. Petersburg, Russia. [1]Corresponding author: e-mail: payevsky@zin.ru

Turdus thrushes are important quarry species in Western Europe (McCulloch et al. 1992), with annual bags comprising many tens of millions of birds (Aebischer et al. 1999, Ricci 2001). Hunting is evidently a significant cause of mortality to song thrushes *Turdus philomelos.*

The migratory route of several thrush species from the populations of north-western Russia and Finland passes through the Eastern Baltic (Payevsky 1973). One of segments of this route is the Courish (=Curonian) Spit in the Kaliningrad Region in the south-eastern corner of the Baltic Sea, where massive bird trapping provides a large data set on migrating birds and allows an analysis of their demographic parameters. The aims of this paper are: (1) to compare recovery circumstances of song thrushes in different countries of Europe; (2) to determine the age distribution of song thrushes in hunting bags; and (3) to estimate age-specific survival rates and to discuss the effects of hunting on song thrush population dynamics.

Material and methods

Birds have been trapped and ringed annually since 1957 by the staff of the Biological Station Rybachy of the Russian Academy of Sciences Zoological Institute. From April until November birds are caught at two sites on the Courish Spit: at the permanent 'Fringilla' field station (55°05' N, 20°44' E) and at the Rybachy field site on Rossitten Cape (55°09' N, 20°51' E). At 'Fringilla' birds are trapped in stationary Rybachy-type traps (for a detailed description of the traps see Payevsky 2000), and at the Rybachy site birds have been mist-netted since 1993.

Lists of long-distance recoveries of birds on the Courish Spit in 1956–1999 have been published by Payevsky (1973) and Bolshakov et al. (1999, 2000, 2001). The latter three publications gave all recoveries available in the end of 2000. We have analysed a total of 358 recoveries of song thrush from 22 907 birds ringed. Most thrushes were ringed during migration.
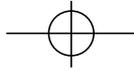
These migratory birds belong to populations from Finland, north-western Russia and the eastern Baltic States.

All trapped birds were aged using plumage characteristics, moult and wear, following Svensson (1970, 1992) with our additions (Vinogradova et al. 1976). The main age character when ringing passage populations of song thrushes was the incomplete replacement of the greater coverts in immatures.

To calculate the age distribution of song thrushes in the hunting bag, we considered seasons of the avian annual cycle, not calendar seasons. According to data on breeding biology (Haartman 1969, Malchevsky & Pukinsky 1983) the average hatching date of these populations is 10 June. As all birds hatch between May and July, we have denoted the immature age group as birds after independence from their parents until 10 June of the next calendar year. The average age of our immature thrushes at ringing is 3 months 20 days.

To estimate survival rate, we used passage thrushes ringed only between 10 September and 21 October (autumn peak in Fig. 1). Accordingly, the midpoint of the ringing period falls on 30 September. The formal condition that the sampling period must be short as compared to the period between sampling occasions (Brownie et al. 1985) was thus observed. Survival probability (S) was defined as the probability that a bird alive in year i survives until year $i+1$. First-year survival probability was defined as the probability that a bird alive at the midpoint of the ringing period (30 September) survives until 10 June (the middle of their first breeding season) and therefore covers 8 months and 20 days. Adult annual survival probability was defined as the

probability that a bird alive on 10 June survives until 9 June of the next year and therefore covers 12 months. The data were organised in accordance with these periods to make our results comparable with the published data of the British trust for Ornithology (Thomson et al. 1997, 1999).

We used 178 dead recoveries of full-grown (first year) thrushes during 1958–1978 to estimate survival rate. We modelled survival and reporting rates using program MARK v. 2.1 ('recoveries only' option; Cooch & White 2001, White & Burnham 1999). To estimate survival rate we applied age-dependent models (Freeman & Morgan 1992; Catchpole & Morgan 1996) due to young-only data being available. Age-dependent survival models were fitted by MARK using the parameter index matrix and sine link function.

The final model was selected by starting from a 'global' model in which first-year survival depends on the year of ringing and adult annual survival probability varies with the age of bird, and then selecting between a variety of a set of alternative submodels. We believe that for song thrushes aged two years or older, age-dependence of annual survival probability (S) was not necessary as it is generally considered that survival stabilises by the age of two years. Thus we chose the 'sub-global' model (using the terminology of Freeman & Morgan 1992) in which first-year survival probability varies with year of ringing, and age-dependence of survival for adult birds aged ≤ 2 years and reporting probability (r) varies with year of recovery. We assume that all birds aged > 2 years have the same annual survival probability. The limitation of the age-dependent models is that the age-specific reporting rate cannot always be estimated.
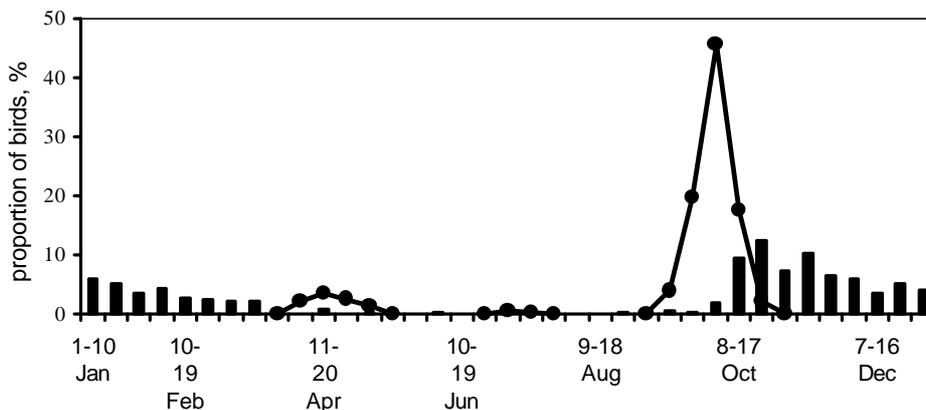
Figure 1. Relationship of ringing seasons of song thrushes (curve) and recovery period (histogram).
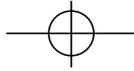
It is well known that first-year reporting rate may be higher than the adult reporting rate, which may potentially cause a serious bias in the estimate of first-year survival. Freeman & Morgan (1992), however, found that this bias is small and may be ignored in practice. For British song thrushes, Thomson et al. (1997, 1999) found no evidence that reporting probability varies between first-year and adult birds. Even though it was later shown that reporting rate differs between age classes (W. Peach, pers. comm.), we believe that the use of models based on age-independent reporting rate remain satisfactory.

To describe the various Freeman-Morgan submodels we use following notation: S^{FY} denoted first-year survival probability, S^{AD1} denoted constant annual survival probability of adult birds aged 1 year, S^{AD2} denoted constant annual survival probability of adult birds aged 2 years or older, S^{AD} denoted constant annual survival probability of adult birds since age of 1 year. Symbol (t) refers to general dependence on time, and (.) refers to no dependence on time. For reporting rates symbol (t) refers to the year of recovery.

A simulation approach was used to calculate the goodness-of-fit between our data and the global model. We used c (variance inflation factor; Cooch & White 2001) as a measure of overdispersion within each dataset, and to adjust sampling variances. We calculated c as the observed deviance from the global model divided by the mean deviance from 500 parametric bootstrap simulations of the global model (Cooch & White 2001). A distribution of expected c for the global model was generated from 500 simulations. Observed c was then compared to the distribution of simulated values to determine whether the global model was an adequate fit to the data. Goodness-of-fit tests based on simulations indicated that the global model was a satisfactory starting point for all datasets (P-values > 0.05). We proceeded to improve model fit by fitting nested models with reduced numbers of parameters. Model selection was based on the difference in QAICc (quasi-Akaike's Information Criterion; Cooch & White 2001) values between models (ΔQAICc). The best fitted model had a ΔQAICc of zero. We chose a model with constant survival rate for estimating survival probability for all datasets. Other statistical tests followed Sokal & Rohlf (1998).

Results and discussion

Recovery rate and recovery dates

The overall recovery rate of song thrushes is very low (no more than 1.5–2 %), as in other passerines. On the basis of 1958–1999 data there is a correlation between the numbers of birds ringed and number of recoveries (r_s = 0.72, n = 41, P < 0.001). Comparison of ringing dates on the Courish Spit and recovery dates indicates seasons of most intensive contacts of thrushes with humans (Fig. 1). The number of recoveries peaks during winter months, corresponding to the hunting season in west European countries. Song thrushes are not a quarry species in Russia.

Finding circumstances of ringed song thrushes in different countries

Of 358 recoveries of song thrush available to us, 255 (71 %) were reported as 'shot'. Cases reported as 'caught, further fate unknown' (29 recoveries), and 'manner of recovery unknown' (23 recoveries) are also likely to belong to this category. This assumption is based on the existence of a popular tradition of netting migratory songbirds for food, especially in Italy (Ghigi 1958). It is probably no exaggeration to assume that of all recovered thrushes with rings, 307 (86 %) were killed by hunters and fowlers.

Differential hunting pressure on thrushes between countries is clearly shown by the proportion of all finding circumstances that comprise hunting recoveries. The highest proportion is found in Italy (92.9 ± 2.8 %), France (92.3 ± 2.1 %), Spain (81.1 ± 4.1 %), and Portugal (72.7 ± 13.4 %), where thrushes are evidently subject to considerable hunting pressure. The difference from other European countries, where the proportion of birds killed is only 27.7 %, is highly significant (χ^2 = 59.9, d.f. = 1, P < 0.001).

Age distribution of song thrushes in the hunting bag

Among nocturnal migrants ringed on the Courish Spit the vast majority of individuals captured in autumn are immatures hatched in the current year (Payevsky 1985, 1998). This phenomenon of a very low proportion of adults in captures has been termed the 'coastal effect',
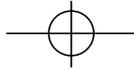
Table 1. Age distribution of song thrushes in the hunting bag.

Age (years)	Exact age*	Inexact age**
0 (immature)	106	81
1	26	35
2	10	7
3	4	17
4	3	7
5	4	3
6	0	1
7	0	1
8	1	0
9	0	0
10	0	0
11	0	0
12	0	0
13	0	1

* the EURING codes 1, 3, and 5 in the process of ringing.
** the EURING codes 2, 4, and 6 in the process of ringing.

from the similar example of passerine birds trapped at coastal sites in North America (Ralph 1978). Disregarding the causes of such an effect, it should be emphasised that it concerns only nocturnal migrants as opposed to species that migrate by day. Such a high proportion of immature birds is not consistent with the potential productivity of the populations involved. The impact of the 'coastal effect' on demographic studies of migrants is apparent, in that we cannot use the trapping data of nocturnal migrants in studies of age structure and its annual variations.

The exact age of passage song thrushes has been recorded during ringing on the Courish Spit since the early 1970s. It became immediately apparent that the bulk of birds captured by us are immatures. Trapping data for 1972–1995 have shown that in some years not a single adult song thrush was captured. Of 11 544 song thrushes trapped in those years, adults comprised on average 6.5 % during autumn and 19.2 % during spring (Payevsky 1998).

Although most song thrushes ringed on the Courish Spit are immatures, the exact age was not known in all cases. Therefore when we calculated the age distribution of thrushes in hunting bags, birds with known and unknown age at ringing (307 birds in total) were trea-

ted separately (Table 1). As the proportion of adult song thrushes in autumn does not exceed 7 % on average, a safe assumption is that of all birds aged as 'full grown', c. 93 % were immatures. We can therefore assume that over 60 % of song thrushes hunted are immatures, and that the immature/adult ratio in the hunting bag is 1.6 (Table 1).

Despite these calculations, some doubt remains whether the age distribution in the hunting bag indeed reflects the true proportion of age classes in nature. Although immatures and adults are shot in equal proportions, we have no information on adults just because they have not been ringed. It may be assumed, however, that immatures are more likely to be shot due to their inexperience.

Some published data sets on breeding performance of thrushes (Haartman 1969, Malchevsky & Pukinsky 1983, Payevsky 1985) suggest that the mean productivity of the song thrushes studied in north-western Russia and Finland does not exceed 3 young fledged per breeding pair per breeding attempt (estimate based on clutch size of 4.3–5.2 eggs, breeding success of 42–61 % and 10–20 % of pairs which have a second breeding attempt after a successful first brood). Thus, the immature/adult ratio just after breeding season should be c. 1.5. This figure is very close to that obtained from the recoveries (1.6).

Survival rates of song thrushes

In a number of European countries songbird hunting was legally restricted in 1979 (McCulloch et al. 1992). We have therefore analysed separately the survival rates of thrushes before 1979. Furthermore, because an understanding of the impact of hunting on survival rates may be best achieved by comparing the rates between hunted and non-hunted populations (Aebischer et al. 1999), we have compared the survival rates of song thrushes that were ringed in the Eastern Baltic and spend their winter in continental Europe and the Mediterranean regions with the published data on survival of song thrushes on the British Isles over the same time periods (Thomson et al., 1997, Siriwardena et al., 1998). Most British thrushes remain on the islands all year round, and only some birds from southern England migrate to France and Spain (Ashmole 1962, Cramp 1988). The main difference in the life cycles of these birds is that within British Isles they are not hunted.
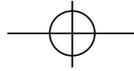
Table 2. Selection of Freeman-Morgan age-specific models for the song thrush data for 1958–1978. Model selection based on c=1.485.

Model	ΔQAICc	QAICc weight	Model likelihood	#Par	QDeviance
$S^{FY}(.)\ S^{AD}\ r(t)$	0.00	0.49283	1.0000	23	70.590
$S^{FY}(.)\ S^{AD1}\ S^{AD2}\ r(t)$	1.38	0.24670	0.5006	24	69.961
$S^{FY}(.)\ S^{AD}\ r(.)$ (minimal)	2.19	0.16479	0.3344	3	112.930
$S^{FY}(.)\ S^{AD1}\ S^{AD2}\ r(.)$	3.31	0.09408	0.1909	4	112.049
$S^{FY}(t)\ S^{AD}\ r(.)$	12.50	0.00095	0.0019	23	83.093
$S^{FY}(t)\ S^{AD1}\ S^{AD2}\ r(.)$	13.96	0.00046	0.0009	24	82.535
$S^{FY}(t)\ S^{AD}\ r(t)$	16.64	0.00012	0.0002	43	46.857
$S^{FY}(t)\ S^{AD1}\ S^{AD2}\ r(t)$ (global)	17.56	0.00008	0.0002	44	45.750

The results of fitting Freeman-Morgan age-specific models are shown in Table 2 and a comparison of survival rates of hunted and non-hunted populations of song thrushes in Table 3. The use of age-dependent models made it possible to estimate the survival rates of immature and adult thrushes on the basis of ringing data on immatures only. The first-year survival rate of Baltic birds wintering on the continent appeared to be slightly below the first-year survival rate of British song thrushes. The values of first-year survival rate obtained by us (Table 3) are in the lower part of the range of first-year survival rates (0.371–0.528) reported for British song thrushes for 1962–1995 (Siriwardena et al. 1998).

To compare our data on first-year survival rate with the published British data, it is necessary to use comparable periods. In Britain, the first-year survival rate was estimated for the period between 2 and 12 months old. Our data refer to the period between 3 months 20 days old and 12 months, and the difference of 1 month 20 days between studies must be taken into account in any comparison. We used the published data on British song thrushes (Thomson et al. 1997, 1999) to make this correction. In Britain from 1962 to 1975 the survival rate was 0.376 from fledging until 2 months old, and 0.484 between 2 and 12 months old. Survivorship until 12 months after fledging is therefore 0.376*0.484 = 0.182. We are interested in the relative frequency of birds that survive until 3 months 20 days. We used linear interpolation between 0.376 and 0.182 and estimated the survivorship to 3 months 20 days as 0.344. Then the survival rate between 3 months 20 days and 12 months will be 0.182/0.344 = 0.529 in the British birds. This value is directly comparable with estimate of 0.411 for Baltic song thrushes (Table 3).

Table 3. Survival rates of song thrushes in intensively hunted populations (birds wintering on the European continent) and in non-hunted populations (British Isles).

Region and years	First-year survival (SE)	Annual adult survival (SE)	Source
Continent			
1958–1978	0.368 (0.051)	0.593 (0.059)	Authors' data
1962–1975	0.411 (0.065)	0.561(0.085)	Authors' data
1967–1975	0.420 (0.087)	0.633 (0.120)	Authors' data
British Isles			
1962–1975	0.484 (0.020)	0.573 (0.011)	Thomson et al. 1997
1967–1975		0.584	Thomson et al. 1997
1962–1993	0.450 (0.014)	0.571 (0.009)	Thomson et al. 1997
1962–1994	0.463 (0.011)	0.563 (0.007)	Siriwardena et al. 1998
1975–1993	0.405 (0.022)	0.568 (0.013)	Thomson et al. 1997
1985–2000	0.590		Robinson et al. 2002
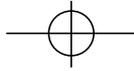
Our data on first-year survival rate (Table 3) are substantially lower than figures reported from Britain. In contrast, adult survival rates in the Baltic area and in Britain are similar. At the same time, the values of adult annual survival rate obtained by us (Table 3) are considerably higher than those reported from the adjacent regions (Aebischer et al. 1999).

Compensatory reproduction and population status

It is not immediately clear to what extent the survival rate is governed by hunting pressure. Along with hunting, a number of other factors affect survival, many of which are density-dependent, and it is virtually impossible to isolate the importance of hunting pressure alone. The problem is best approached by a comparing estimates of survival rates from hunted and non-hunted populations, as in our example with Baltic and British song thrushes. In this case, however, different living conditions may influence the annual survival rate at least as profoundly as hunting pressure. For instance, these two populations differ in migratory habits. Winter movements, if any, of British thrushes are an order of magnitude shorter than the movements of their conspecifics from Finland and Eastern Baltic. It has been suggested that 'relatively low survival rates may be an intrinsic feature of largely migratory song thrush populations, and the apparently high index of hunting loss may simply be a reflection of the passage of the birds through the Mediterranean' (Aebischer et al. 1999). Accordingly, seasonal migrations and/or hunting pressure may be the factors which reduce the survival of song thrushes from the Eastern Baltic. That migration can cause additive mortality has been shown in robins *Erithacus rubecula* by Adriaensen & Dhondt (1990). On the other hand, a study of the adaptive significance of seasonal migration in various bird species showed that mortality during migration is no higher than during the winter period (Payevsky 1999).

In some studies, e.g. on willow grouse *Lagopus lagopus*, a significant decrease has been shown in survival rates in areas with a strong hunting pressure (Smith & Willebrand 1999). Decreases in annual survival rates of British blackbirds *Turdus merula*, song thrushes and mistle thrushes *T. viscivorus* were found only in years when populations declined. In the song thrush this effect occurred in juveniles only and was due to severe

weather in winter (Baillie 1990, Thomson et al. 1997, Siriwardena et al. 1998, Wernham et al. 1998). Other studies, especially of waterfowl, have shown that hunting mortality is compensated for by other forms of mortality (Burnham & Anderson 1984, Mihelsons et al. 1985). In other words, mortality due to hunting is not additive to the natural mortality, as long as the former does not exceed a certain threshold. Productivity and mortality are compensated reciprocally, presumably on the basis of density-dependent regulation mechanisms.

Legislative restrictions on hunting songbirds established in 1979 seem to have had a very limited effect on the real hunting pressure. Some decrease in the reporting rate of rings is believed by many authors to be due not to a smaller hunting pressure but to the fear of sanctions (McCulloch et al. 1992). In our data, however, 65 % of recoveries after 1979 were still reported as 'shot'. We therefore believe that our conclusions concerning the impact of hunting on the survival of thrushes will also be relevant for the period after the formal hunting ban.

The results of our comparison of survival rates in different regions and years imply that if hunting does induce some additive mortality of song thrushes, it occurs in immatures only. Compared with adults, first-year birds seem to be more vulnerable to an adverse environment. It has been shown for British song thrushes that 'first-year survival was lower during years with cold or dry winters and adult survival was lower during years with cold winters' (Thomson et al. 1997). What could be the reason under these age-related differences? We suggested above that immatures are more vulnerable because they migrate for the first time in their lives.
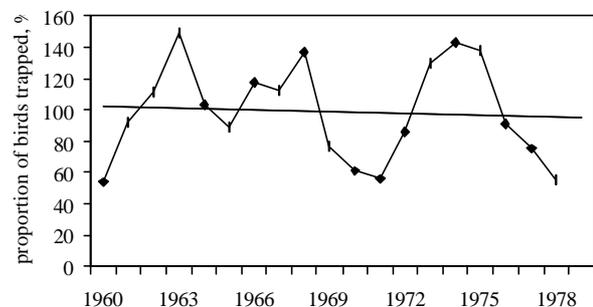
Figure 2. Fluctuations of song thrush numbers on the Courish Spit in 1960–1978 (total n = 5622). Birds were trapped by standard Rybachy-type traps, located in the same sites throughout (Payevsky 1985).
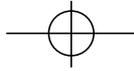
On the other hand, there is no reason to believe that Baltic thrush populations are endangered due to hunting. During the period 1958–1978 numbers of passage song thrushes in the Eastern Baltic fluctuated without showing significant trends (Fig. 2), and similar patterns for song thrushes during these years were also observed in Finland and Sweden (Järvinen & Väisänen 1978a,b, Hjort et al. 1981).

In conclusion, we have shown that in the Baltic area adult survival rates did not differ from the values obtained for the British populations, whereas first-year survival was lower than in British birds. This implies the occurrence of compensatory hunting mortality for adult song thrushes. The absence of any indication that Baltic populations have shown a decline suggests that hunting mortality of first-year thrushes may be balanced by a higher productivity. We can only guess which population mechanisms cause such higher productivity. The published breeding data (Haartman 1969, Malchevsky & Pukinsky 1983, Payevsky 1985, Cramp 1988) suggest that neither clutch size nor brood size show a marked difference between these populations. The parameter most difficult to measure in field studies of any bird species is the proportion of normal second clutches laid after a successful rearing of the first brood. The reason is that they look very similar to the repeat clutches made after nest loss. The only plausible assumption is that in the Baltic populations which are subject to a hunting pressure, more pairs are double-brooded annually than in other populations.

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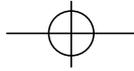
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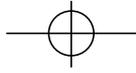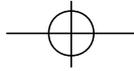
A quantitative estimate of the spatial and temporal distribution of nocturnal bird migration in south-eastern Europe – a coordinated moon-watching study

Pavel Zehtindjiev[1] **and Felix Liechti**[2]

In SE Europe, the spatial and temporal distribution of nocturnal migration is hardly known. With the moon-watching technique the passage of 5603 nocturnal migrants was recorded during 419 observation hours at 29 sites spread over Bulgaria, SE-Romania and northern Greece. Mean migratory traffic rate was 1400 birds.km^{-1}.h^{-1} in autumn and 900 birds.km^{-1}.h^{-1} in spring. Migration intensity was similar along both E-W and N-S gradients. Flight directions were virtually opposite between seasons, with a slight shift from SSW to S during the autumn and from NNE to N during the spring. These results indicate that a high proportion of nocturnal migrants along the eastern flyway do not circumvent the eastern Mediterranean Sea, but crosses the sea on a broad front. This is in contrast to the migration along the western flyway, where a majority of mainly long distance migrants take southwesterly directions towards the Iberian Peninsula and thus avoid a long sea crossing.
Key-words: Nocturnal migration, moon-watching, migratory intensity, flight direction, SE-Europe.

[1]Institute of Zoology in Bulg. Acad. of Sciences, Sofia 1000; [2]Swiss Ornithological Institute, CH–6204 Sempach. Corresponding author: kalimok@einet.bg

Nocturnal bird migration over Europe is dominated by small passerines (Bloch et al. 1981, Rabenold 1993), with many of them migrating long distances to sub-Saharan Africa. Their migratory routes have been studied through various ringing schemes for several decades (Zink 1973, Zink & Bairlein 1995). Based on these ringing results, Zink suggested that a majority of trans-Saharan migrants circumvent the Mediterranean Sea to the east and the west. In contrast, Moreau (1972b) proposed that most species cross the Mediterranean Sea and the Sahara desert on a broad front. Nocturnal passage has been observed directly at numerous sites by means of radar, moon watching and passive infrared techniques (see Bruderer & Liechti 1999 and references therein). In autumn, migration along the western flyway is directed on a broad front towards the southwest, resulting in a high migration intensity over the Iberian Peninsula, compared to a reduced long-distance migration over the western Mediterranean Sea. Also in spring migration over the island of Mallorca

was only one fifth of that over the Spanish mainland (Bruderer & Liechti 1999). Hence, along the western flyway the Mediterranean Sea is circumvented by a notable proportion of nocturnal migrants. Up to now, only few data have been available for the European part of the eastern flyway (except Adams 1962, Bolshakov et al. 1998, Casement 1966, Szép 1992). It was therefore not possible to decide, whether the European branch of the eastern flyway is mainly directed towards the Middle East, or crosses the eastern basin of the Mediterranean Sea on a broad front. The aim of this study was to fill part of this gap in SE Europe, mainly the Balkan area.

Methods

This first co-ordinated large-scale research on nocturnal bird migration in the Balkan region was carried out in the autumn of 2000 and the spring of 2001.
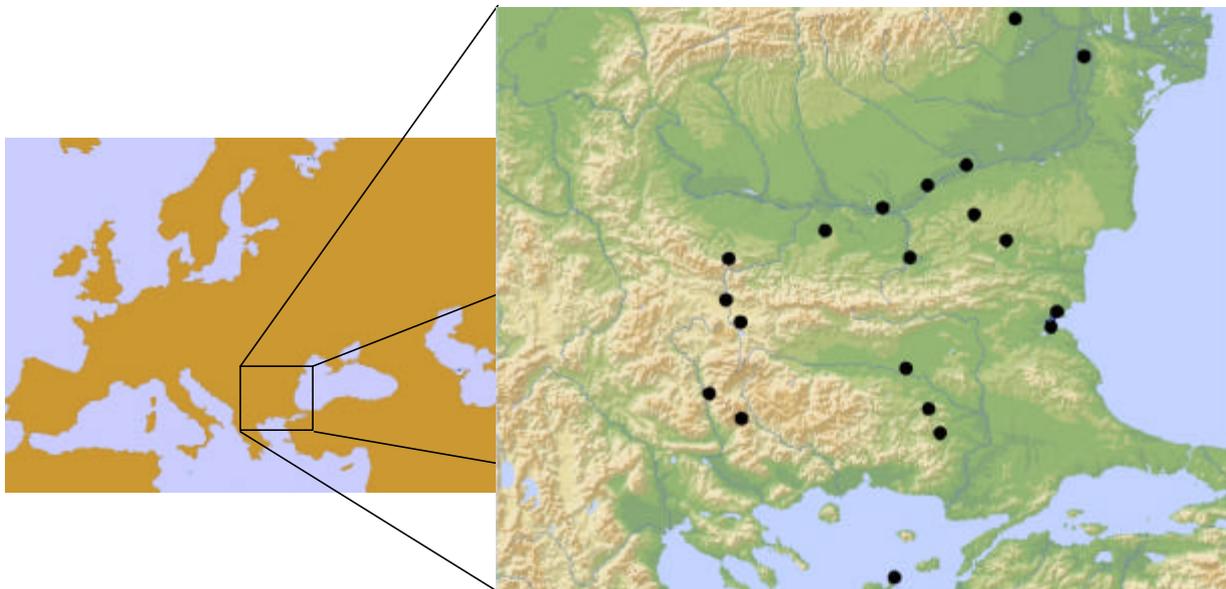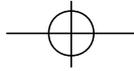
**Figure 1.** Map of the observation area in southeastern Europe. Black dots indicate observation sites.

Simultaneous moon-watch observations were carried out at 28 sites (Fig. 1) during the periods of full moon in autumn (12–18 August; 9–15 September; 10–16 October) and spring (7–12 March; 5–8 April; 4–10 May). Depending on the meteorological conditions and the availability of the observers involved, the number of the sites for simultaneous observations varied from 7 to 12. Only observations from sunset to 8 h after sunset were included. In the autumn of 2000 we collected observations of 3815 silhouettes during 242 h of observations from 19 sites, spread over 7 nights each in August, September and October (Table 1). In the spring of 2001, 1696 silhouettes were counted at 16 different sites during a total time of observation of 167 h, spread over 7 nights in March, 5 nights in April and 7 nights in May. We also included previous observations from 4 nights in mid-May 2000. Wind speed and direction were taken from the upper air wind maps (850 mbar) for midnight available on the internet (Mesoscale Alpine Program MAP: http://www.cmirl.ge.infn.it/mappe/bolam/bolam 21/).

Data on the passage of nocturnal bird migration were collected by the moon-watching method (Lowery 1951), following the guidelines given by Liechti et al. (1996b). While watching the disk of the full moon by telescope the observer recorded the relative size, the entrance and exit of all bird silhouettes passing through

the disk. Flight directions were calculated according to the position of the moon, under the assumption that the bird was flying horizontally. Migration traffic rate (MTR) was computed with respect to the estimated distances of individual birds, their flight directions and the position of the moon (Liechti et al. 1996b). Observations were included only when moon elevation was above 15°. Distance estimates were based on the relative size classes calibrated by parallel observations with a pencil-beam radar (Liechti et al. 1995, Liechti 2001). This indicates the approximate height distribution of nocturnal bird migration. However, real size differences between birds were ignored.

Statistics

For MTR means and standard deviation are given. For linear statistics and variance analysis the MTR-values were log-transformed. Analysis was performed with the software package SPSS© (v. 9.0.0). Circular statistics were calculated according to Batschelet (1981). Mean directions were calculated from individual flight directions. As the surveyed space is smaller at short than at long distances, large silhouettes (short distance) are given more weight than small ones with respect to migratory traffic rate. We decided not to weight the frequency of directions accordingly, because we know of
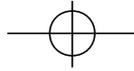
Table 1. Location of the observation sites and data collected at each site during autumn 2000 and spring 2001.

| Location	Latitude/Longitude	Autumn				Spring			
		no. of nights	hours	no. of birds	mean MTR	no. of nights	hours	no. of birds	mean MTR
Bistrica	42°03'N, 23°11'E	1	1	11	1442				
Braila	45°27'N, 27°09'E	12	16	226	1185				
Burgas	42°31'N, 27°23'E	6	8	75	957	10	20	71	236
Dimitrovgrad	42°03'N, 25°36'E	15	32	482	1575	1	2.5	20	1101
Dolni Bogrov	42°41'N, 23°30'E					1	3.0	35	1407
Elena	41°51'N, 25°48'E					1	2.6	27	1179
Gorna Oriahovica	43°07'N, 25°40'E	1	2	11	473				
Iskar	42°30'N, 23°34'E	2	3	58	2300				
Izvorovo	41°58'N, 26°08'E					1	2.5	30	1052
Kresna	41°48'N, 23°11'E	3	4	62	1173				
Limnos	40°00'N, 25°25'E	2	7	222	2773				
Lom	43°05'N, 23°14'E					5	11.6	102	777
Madjarovo	41°39'N, 25°53'E	8	19	196	1067	5	6.4	60	1105
Malino	41°24'N, 26°01'E	7	10	122	1219				
Milanovo	43°08'N, 23°25'E	7	13	149	1068	6	8.1	51	694
Nova Cherna	43°59'N, 26°28'E	17	26	634	2075	12	20	341	1354
Pirin	41°48'N, 23°34'E	3	4	23	555				
Pleven	43°25'N, 24°37'E	13	17	162	801	6	10.5	57	456
Plovdiv	42°25'N, 24°37'E					9	15	144	1173
Poda	42°30'N, 27°28'E	2	2	27	1087				
Purvomai	42°20'N, 24°40'E					4	8.1	41	557
Razgrad	43°31'N, 26°31'E					2	5.5	122	1497
Rusenski Lom	43°50'N, 25°57'E	2	4	86	1744				
Shtit	41°49'N, 26°22'E					2	2.3	96	2932
Shumen	43°16'N, 26°55'E	9	13	370	2103	14	26	176	746
Sofia	42°41'N, 23°19'E	17	57	859	1525	11	27.9	382	1228
Svishtov	43°37'N, 25°21'E	4	5	35	849	10	20	71	236
Traianu	45°02'N, 28°02'E	1	1	11	1442				
total		132	244	3821	1412*	100	192	1826	949*

* Mean calculated after means per site and night.

no circular statistical test which would allow to consider this weighting. We checked both ways of calculating mean directions. Results obtained are very similar. To us, the numbers of observations is suited much better to verify the level of significance than the calculated sum of MTR. Individual flight directions were analysed using general linear models. For this procedure flight directions were restricted to the seasonally appropriate semicircle, and hence flight direction was treated as a linear variable. We are convinced that this simplification is justified and does not compromise our robust results.

Results

Autumn

Mean migratory traffic rate (MTR) in autumn was 1412 ± 947 birds.km^{-1}.h^{-1}, n = 131 (Table 1). Although mean MTR in August (1021 ± 492 birds.km^{-1}.h^{-1}, n = 48) was considerably lower than in September (1667 ± 1070, n = 46) and October (1587 ± 1085, n = 37), a significant difference occurred only between August and September (ANOVA: n = 131, $R^2 = 0.061$, P = 0.018; Scheffe-test: Aug v. Sep P = 0.02; Aug v. Oct P = 0.231; Sep v. Oct P = 0.640). We analysed mean MTR per night and site with respect to longitude and latitude for each
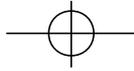
month. In August, migratory intensity increased significantly towards the east (linear regression n = 48, R^2 = 0.095, P = 0.033; Fig. 2a), whereas no geographical trend could be detected for September and October (Figs 2b and 2c). Flight directions varied considerably during autumn migration (Fig. 3). Individual flight directions (Fig. 3a) as well as means per night (Fig. 3b) and means per site (Fig. 3c) tended to be more westerly in August than in September and October.

13 % of all individuals observed flew in seasonally inappropriate directions (<90° or >270°) and were excluded from further analysis. In the general linear model, latitude, flight altitude and month were significantly correlated with flight direction, whereas longitude contributed no effect to the model (ANCOVA: n = 3317, df = 4, F = 16.0, P < 0.001). Flight directions shifted from SSW to SSE with decreasing latitude (P < 0.001), and increasing flight altitude (P = 0.002). In August flight directions were more westerly (i.e. SSW) than in September and October (P < 0.001). In addition, the over- all scatter of flight directions decreased significantly from August to September, and from September to October (P < 0.001; parametric test for concentration parameter).

Spring

MTR in spring was 949 ± 724 birds.km⁻¹.h⁻¹, n = 93. Mean MTR in March (647 ± 565 birds.km⁻¹.h⁻¹, n = 27) was considerably lower than in April (1025 ± 710, n = 40) and May (1146 ± 829, n = 26). Differences between March and both April and May were significant (ANOVA: n = 92, F = 3.5, df = 2, P = 0.005; Scheffe-test: Mar v. Apr P = 0.013; Mar v. May P = 0.019; Apr v. May P = 0.945). Neither mean MTR per night nor per site was correlated with either latitude or longitude (Figs 4b and 4c).

In general, flight directions during spring migration were less scattered than in autumn (Fig. 5). Individual flight directions (Fig. 5a) as well as means per night (Fig. 5b) and means per site (Fig. 5c) tended to be more easterly in March (i.e. NNE) than in April and May.
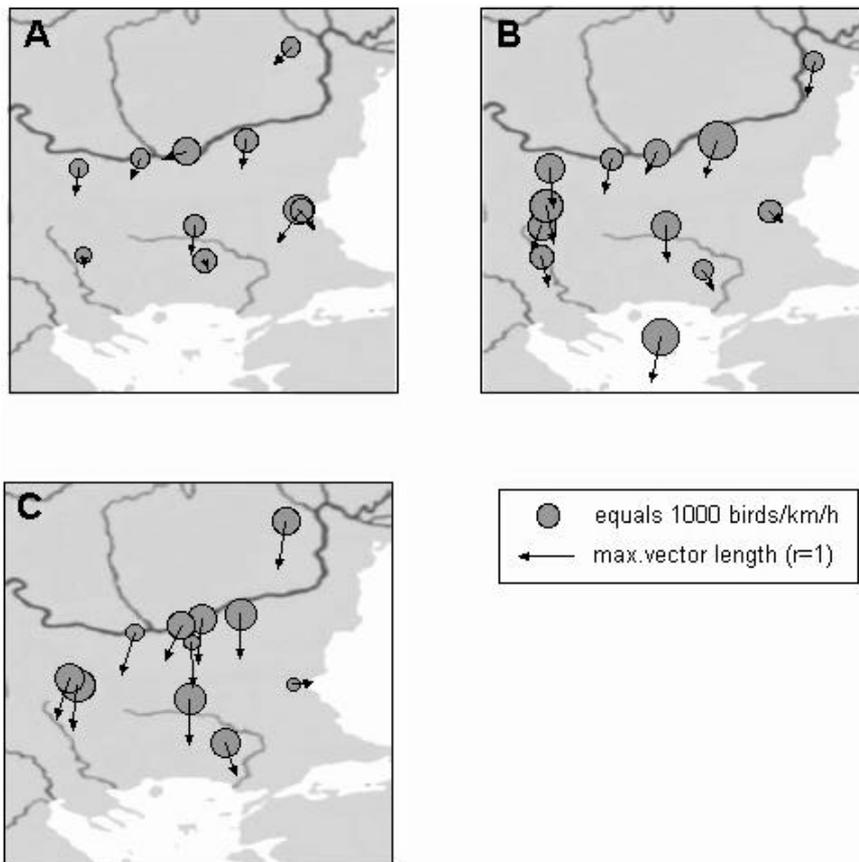
Figure 2. Distribution of mean migration traffic rate (MTR) per site and mean flight direction for the three observation periods in autumn 2000. (A) 12–18 August; (B) 9–15 September; (C) 10–16 October. MTR is represented by the area of the circle. Flight direction is indicated by the mean vector, the length of the arrow is proportional to the concentration of the distribution of individual directions.
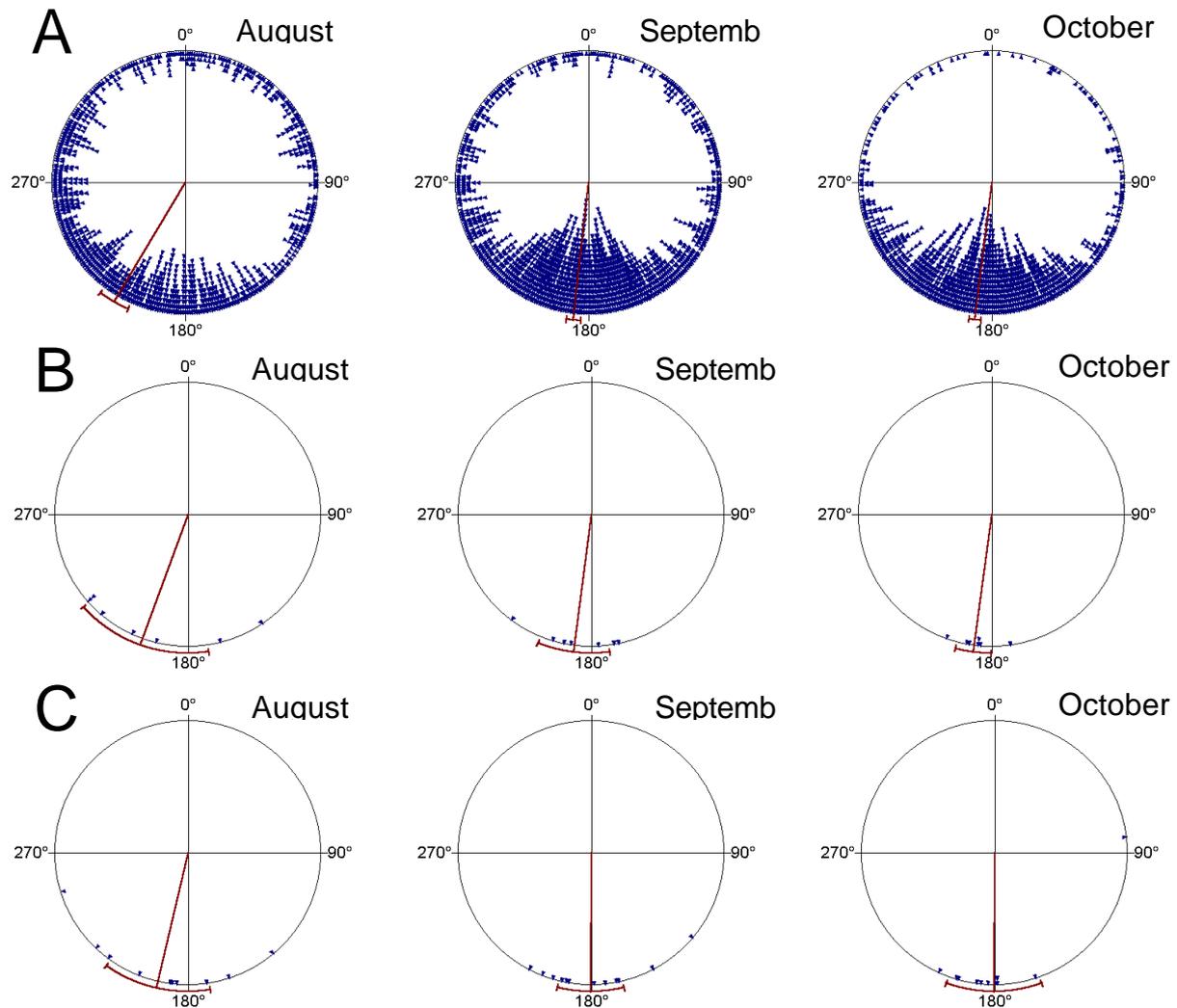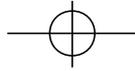
Figure 3. Distribution of flight directions in autumn. (A) individual flight directions August (mean = 211°, r = 0.35, n = 1073), September (186°, 0.61, 1562) and October (187°, 0.75, 1180); (B) mean flight directions per night for August (200°, 0.87, 7), September (187°, 0.96, 7) and October (188°, 0.99, 7); (C) mean flight directions per site for August (193°, 0.86, 10), September (180°, 0.93, 12) and October (180°, 0.88, 11).

8 % of all individuals observed flew in seasonally inappropriate directions (>90° or <270°) and were excluded from further analysis. In the general linear model, latitude and month were significantly correlated with flight direction, whereas longitude and flight altitude did not contribute significantly to the model (ANCOVA: n = 1555, df = 3, F = 17.8, P < 0.001). Replacing latitude by longitude resulted in a similar highly significant model. Flight directions shifted from NNW to NNE with increasing latitude, or as latitude and longitude are correlated, directions shifted similarly with longitude

(P < 0.001). In March and April directions were more easterly than in May (P < 0.001). The overall scatter of flight directions did not differ between months.

Discussion

Autumn
Migratory intensities recorded in our study for autumn were of the same order of magnitude as observed along the western flyway across Germany, northern Italy,
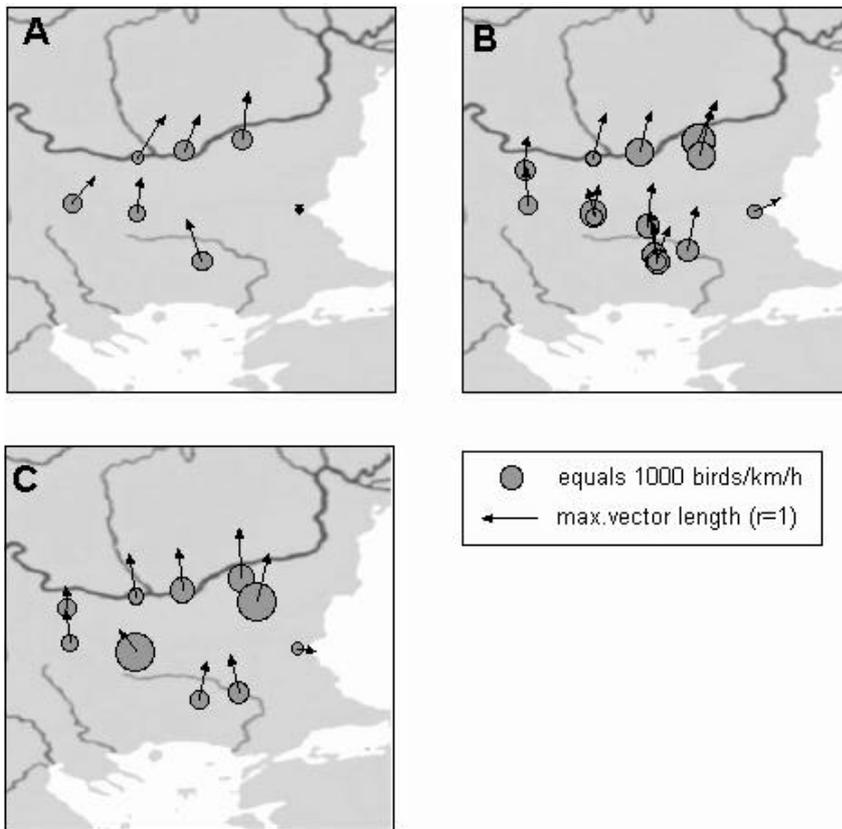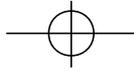
Figure 4. Distribution of mean migration traffic rate (MTR) per site and mean flight direction for the three observation periods in spring 2001: (A) 7–12 March; (B) 5–8 April; (C) 4–10 May. MTR is represented by the area of the circle. Flight direction is indicated by the mean vector, the length of the arrow is proportional to the concentration of the distribution of individual directions.

France and Spain (Bruderer & Liechti 1999, Liechti et al. 1996a). High intensities were observed in September and October with MTRs up to 4000 birds.km^{-1}.h^{-1}, which were similar to maximum values from southern Germany and corresponded to about 60 % of maximum MTRs registered along the border of the Swiss Alps, (Liechti et al. 1996b). Astonishingly, nocturnal autumn migration in the Balkan area is directed S-SSW, thus heading towards the eastern or even the central Mediterranean Sea and the Libyan desert. Southeasterly directions, which would indicate a detour around the Eastern Mediterranean, were not common. Winds available from European weather maps (850 hPa surface) can only give the general pattern of wind within the study area. They were mainly between NW and NE, and were therefore tailwinds for most migrants. In August winds were highly concentrated around NNE with wind speeds between 5 to 10 m/s. This might explain the somewhat more westerly directions but does not explain the large scatter. Similar directions were registered at one of the present observation sites in au-

tumn 1995 (Bolshakov et al. 1998). Our results in September correspond to the data obtained by moon-watching in northern and southern Greece (Bateson & Nisbet 1961). Mean southerly directions were also recorded by radar over the Aegean Sea (Casement 1966). However, observations in the easternmost part of the Mediterranean Sea suggest that some migrants partly circumvent the sea by flying southeast from Turkey across Cyprus to the coast of Israel (Adams 1962, Alfiya 1995).

In August and September the majority of nocturnal passerine migrants consists of trans-Saharan migrants. The proportion of migrants wintering north of the Sahara is likely to be limited, taking into account that these comprise only a few species (Bolshakov et al. 1998). From the trapping data collected in northeastern Bulgaria during the autumn seasons of 1997–2000, 76.5 % of all non-moulting individuals were trans-Saharan migrants, 13.5 % were short-distance migrants, and 10 % were species with intermediate migratory strategies (P. Zehtindjiev unpubl. data). Only 8 % of the trapped birds were species wintering exclusively in eastern Africa
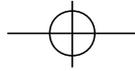
(Moreau 1972a) and migrating SE over Europe. The vast majority of nocturnal migrants in August and September were assumed to be trans-Saharan migrants, while in early October (between 2 and 9 October) the numbers of trans-Saharan and short-distance migrants might be equal. Trans-Saharan migrants showed a higher diversity of migratory directions compared to short-distance migrants. This might be partly due to the high species diversity among trans-Saharan migrants, and hence an increased heterogeneity of migratory strategies, compared to migrants wintering north of the Sahara. However, the decrease in the variability of flight directions with the ongoing season accords with a substantial decrease in reverse movements. The proportion of reversed flight directions decreased during the autumn from 35 % in August to 18% September and 8 % in October. The high proportion of reverse movements in August might be at least partly caused by juvenile birds during their phase of dispersal but still not migrating (Jenni 1984). Between 5 and 10 % of reversed movements seem to be a normal feature of nocturnal migration (Zehnder et al. 2001).
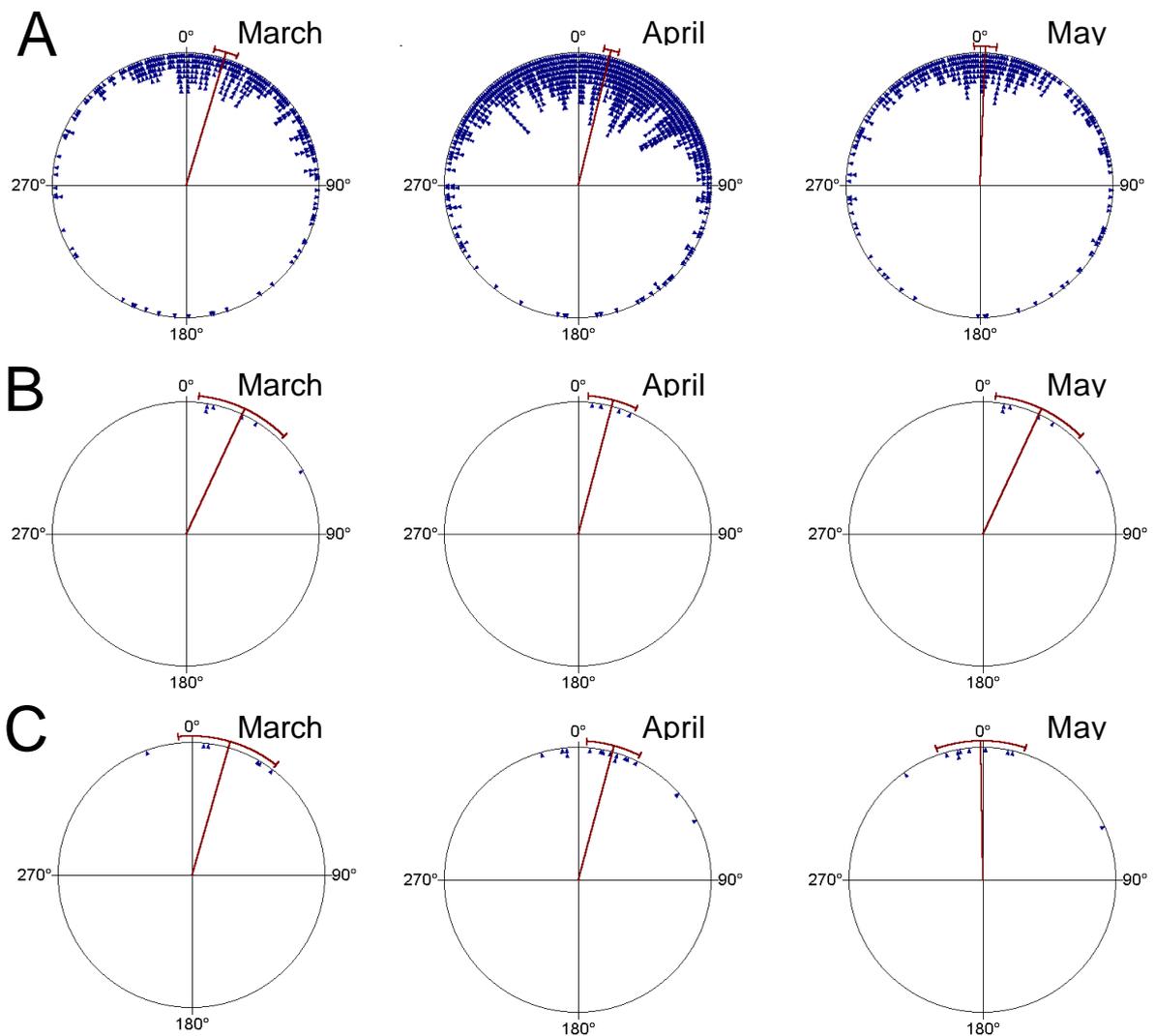
Figure 5. Distribution of flight directions in spring: (A) individual flight directions in March (mean = 17°, r = 0.72, n = 361), April (14°, 0.70, 950) and May (2°, 0.71, 385); (B) mean flight directions per night for March (25°, 0.95, 6), April (14°, 0.99, 4) and May (6°, 0.99, 5); (C) mean flight directions per site for March (16°, 0.94, 6), April (15°, 0.94, 15) and May (359°, 0.91, 10).
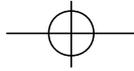
At a finer scale, we could not find any important geographical trend, even though flight directions shifted slightly to the right with latitude in autumn and spring. Because of the lack of consistent data recording at all sites simultaneously we refrain from interpreting these results in detail. Subjectively, we detect an influence of the topography of Balkan Peninsula and adjacent territories on the diversity of flight directions. A strong flow of migrants passing between the Carpathian Mountains and the Black Sea may occur down to southern Bulgaria and northern Greece. Another flow of migration may enter the study area from the NNW across the westernmost southern Carpathian mountains following the West Balkan mountain ranges. Low densities were consistently recorded in the central part of the lower Danube valley (Pleven, Table 1), south of the highest ridges of the southern Carpathian mountains (>2500 m a.s.l.). At Burgas in August, the movement towards the southeast along the Black Sea coast was probably due to the high concentrations of waders in the wetlands flying along the Bulgarian coast. At all the other sites there was no indication by the observers that waders made up a major component of night migration.

Spring
Mean and maximum migration intensities recorded during spring migration were about two-thirds of the autumn intensity. On average the MTRs were higher than those observed along the western flyway (Bruderer & Liechti 1999) and therefore the ratio between spring and autumn migration was higher in the Balkan area, but similar to results gathered by radar in Israel (Bruderer & Liechti 1995). The direction of the night migration in spring was opposite to that in autumn. In March, when short-distance migrants fly through the study area (according to ringing results), flight directions were more towards the northeast than later in the season when trans-Saharan migrants passed through, although the differences in spring between months in absolute terms was relatively small (15°).

On a more detailed scale we could observe a gradient from NNW- to NNE-movements from west to east within the study area. We interpret this as the result of two main migratory streams, one towards the plain between the southern Carpathian mountains and the Black Sea, and the other towards the low hills between the west Balkan and southern Carpathian mountains.

Based on the results above, we may derive a rough quantitative estimate of the spatial and temporal distribution of nocturnal bird migration in the Balkan region. The mean MTR was roughly 1400 birds.km^{-1}.h^{-1} in autumn and 900 birds.km^{-1}.h^{-1} in spring. This suggests that about 900 million birds pass through the study area during autumn season and almost 600 million in spring (average width of 900 km, 8 h of flight per night, 90 nights). We assume that about 80 % of these are trans-Saharan migrants.

The majority of night migrating species occur at the Kalimok Station (Bulgaria) both in spring and autumn. The only exceptions are the collared flycatcher *Ficedula albicollis*, red-breasted flycatcher *F. parva* and pied flycatcher *F. hypoleuca*, which are known to have loop migrations. However, our results suggest that the majority of nocturnal trans-Saharan migrants intend to cross the eastern Mediterranean Sea between Greece and Egypt/Libya in autumn as well as spring. However, to confirm these assumptions more data are need from southeastern Europe and Turkey.

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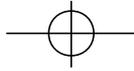
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