

Weather conditions and sexual differences affect the foraging behaviour of the insectivorous Cyprus Wheatear, *Oenanthe cypriaca* (Aves: Passeriformes: Muscicapidae)

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> Abstract

Weather conditions (temperature, cloudiness, wind strength and precipitation) had an influence on the foraging behaviour of the Cyprus Wheatear (*Oenanthe cypriaca*). Under cloudy weather conditions the perch-pounce technique from low perches was used more often while under sunny conditions aerial sallying was used more often. A possible reason is the limited visual range from higher perches during high cloudiness. During higher temperatures and low wind speed aerial sallying from higher perches was preferred presumably because the activity of the ectothermic arthropods is strongly influenced by temperature and wind speed. Sexual differences existed in foraging behaviour. Females used hop-and-peck on the ground more often than males, and males preferred higher perches. This can be explained by a lower exposure to predators and hence lower predation risk that is especially important for females during the breeding season. Furthermore, males and females may occupy different niches during pre-breeding and incubation.

> Kurzfassung

Witterungsbedingungen (Temperatur, Bewölkung, Windstärke und Niederschlag) zeigten einen Einfluss auf das Jagdverhalten des Zypernsteinschmätzers (*Oenanthe cypriaca*). Während starker Bewölkung wurde öfter eine Warte-Boden Jagdtechnik benutzt, während fliegenschnäpperartige Jagd unter sonnigen Bedingungen häufiger war. Ein Grund hierfür könnte die geringere Sichtbarkeit von Arthropodenbeute während starker Bewölkung sein. Während hoher Temperaturen und geringer Windstärke wurde die Fliegenschnäpperjagd bevorzugt, wahrscheinlich deshalb, da die Aktivität von ektothermen Arthropoden stark von Windgeschwindigkeit und Temperatur abhängen. Weibchen nutzen die Hüpf-Pick-Technik auf dem Boden häufiger als Männchen. Männchen bevorzugten dagegen höhere Warten als Weibchen. Dies könnte an unterschiedlichem Prädationsdruck liegen oder aber an der Besetzung unterschiedlicher ökologischer Nischen durch die Geschlechter.

> Key words

Aerial sallying, foraging behaviour, monomorphic species, *Oenanthe cypriaca*, perch-pounce hunting.

Introduction

In this study, we examined the foraging behaviour of the Cyprus Wheatear *Oenanthe cypriaca* (HOMEYER, 1884) in relation to weather and sex. Foraging behaviour has been found to be weather dependent in insectivorous bird species during spring/summer (MURPHY, 1987; SCHAUB, 1996; LOW *et al.*, 2008) and in winter

(EAST, 1980; GRUBB, 1982). For example, Woodchat Shrikes *Lanius senator* used more often aerial sallying during good weather conditions and more often perch-pounce during bad conditions (SCHAUB, 1996; bad weather was classified below 14 °C, rain and or wind > 3 Bft.). Foraging may change due to weather



Fig. 1. Cyprus Wheatears on two different perches (natural vs. anthropogenic). Left: May 2010 at Kathiks, right: May 2010 at Androlikou.

conditions because at low temperatures, birds may alter their behaviour to minimise heat loss (e.g. EAST, 1980). Also, invertebrate prey may alter its behaviour due to environmental changes. Since they are ectothermic their level of activity depends on temperature which, in turn, influences bird behaviour (AVERY & KREBS, 1984; SCHAUB, 1996). In Eastern Kingbirds *Tyrannus tyrannus* hawking movements (which are comparable to the aerial sallying described here) increased with air temperature and decreased with cloud cover (MURPHY, 1987). Male robins *Erithacus rubecula* spent more time foraging on the ground at air temperatures between 0–5 °C than between 6–10 °C (EAST, 1980) and at low temperature male robins changed their perches more quickly. In Northern Wheatears *Oenanthe oenanthe*, perch hunting increased with increasing temperature (KNEIS & LAUCH, 1983).

Also, some authors found significant intersexual differences in foraging behaviour (SELANDER, 1966), and these differences were often described in woodpeckers Piciformes (PASINELLI, 2000; STENBERG & HOGSTAD, 2004; PECHACEK, 2006) and recently have been observed in a monomorphic seabird (Northern Gannet *Morus bassanus*, LEWIS *et al.*, 2002). In songbirds, however, there is only limited evidence for sexual differentiation (FRANZREB, 1983), and most studies were carried out during the period when nestlings were reared (e.g. KRYŠTOFSKOVÁ *et al.*, 2006). For example, in Yellow-rumped Warblers *Dendroica coronata*, males fed at a greater height and used different tree species than females (FRANZREB, 1983); in Com-

mon Redstarts, *Phoenicurus phoenicurus*, females preferred foliage gleaning, while males spent more time perching (KRYŠTOFSKOVÁ *et al.*, 2006). In Black-eared Wheatears, *Oenanthe hispanica*, males preferred higher perches than females (SANTOS & SUÁREZ, 1983). In White-breasted Nuthatches, *Sitta carolinensis*, females foraged significantly higher in vegetation than males during winter (GRUBB, 1982). Intersexual differences have been largely explained with sexual dichromatism in plumage or in morphology, such as bill length, and they seem to be absent or at least reduced in monomorphic species. However, intersexual differences in more or less monomorphic species without morphological sex differentiation may also arise from dominance relationships between males and females (PETERS & GRUBB, 1983; PASINELLI, 2000).

Here, we examined sexual differences in a largely monomorphic insectivorous species, the Cyprus Wheatear. The Cyprus Wheatear is much more monomorphic than, e.g. the Common Redstart or the Black-eared Wheatear. However, sexual differences in foraging have been found in monomorphic songbirds such as the White-breasted Nuthatch (GRUBB, 1982).

Methods

Species. Until 1982 Cyprus Wheatear was treated as subspecies of the Pied Wheatear *O. pleschanka*.

The species status was proposed due to less pronounced sexual dimorphism, morphometric measurements and a clearly different song in comparison to Pied Wheatear (CHRISTENSEN, 1974; SLUYS & VAN DEN BERG, 1982; BERGMANN, 1983); FÖRSCHLER *et al.*, 2010. *O. cypriaca* is the only *Oenanthe* species breeding on Cyprus; Black-eared Wheatear *O. melano-leuca* and Northern Wheatear *O. oenanthe* are regular migrants. In comparison to migrant *Oenanthe*-species, the Cyprus Wheatear is the most arboreal species (RANDLER, 2010; RANDLER *et al.*, 2010), a fact that was assumed because morphometric measurements among *Oenanthe* species showed that *O. cypriaca* seems the most vegetation tolerant species in comparison to the open ground species such as *O. oenanthe* (KABOLI *et al.*, 2007). *O. cypriaca* has small weight (σ : 15.8 g, ϕ : 14.7 g) and size differences (wing: σ : 82.3 mm, ϕ : 81.2 mm; FLINT & STEWART, 1992). Both sexes are similar at first sight but can be distinguished, e.g. by the head and breast coloration (SLUYS & VAN DEN BERG, 1982).

Study area. Cyprus is with an area of 9250 km² after Sicily and Sardinia the third largest and the most south-east located island in the Mediterranean (STAGG & HEARL, 1998). It lies at 34°33' to 35°42'N and 32°16' to 34°36'E (JONES, 2006). The island is dominated by two mountain ranges, the Troodos mountains in the central south-west side rising up to nearly 2000 m and further north, the Kyrenia range rising to over 1000 m. Cyprus has an extreme Mediterranean climate with long, very hot, dry summers and cool, wet, changeable winters (FLINT & STEWART, 1992). This depends on the altitude and although less, on the distance from the sea. The island has a variety of natural vegetation. The majority of its vegetation is maquis; 18 % of the island is woodland (JONES, 2006; FÖRSCHLER & RANDLER, 2009). The work for this study was carried out on the Akamas peninsula in the western parts of the island, NW of Paphos. On the Akamas, vegetation is characterised by high maquis with juniper, a few agricultural areas and large protected areas without agricultural use. Over some parts of the peninsula, land is covered by xerophytic shrubs forming low maquis, or in drier areas, the lower, more open garrigue (JONES, 2006; RANDLER, 2010).

Field work

We observed Cyprus Wheatears during April 2008 and May 2009. Foraging of the target species was observed whenever possible (see SALEWSKI *et al.*, 2003). To avoid pseudo-replication, we used individuals only once for the statistical comparison (HURLBERT, 1984). This was assured by travelling around

the Akamas peninsula and sampling each territory only once. Some other studies used the same individual more than once which inflates sample size. However, we have learnt from HOLMES *et al.*, (1978) that there are individual differences within a given species (American Redstart, *Setophaga ruticilla*). Thus, these individual differences may compromise the statistical analysis. In addition, we only studied adults during pre-breeding and incubation excluding the nestling season (because of food provisioning of the parents).

Foraging variables

Foraging techniques were classified according to KABOLI *et al.* (2006):

- 1) “perch-and-pounce”: the bird scans the ground from a perch and attacks prey by sallying out from the perch;
- 2) “aerial sallying” or “flycatching”: this technique is used to catch flying insects in flight;
- 3) hovering;
- 4) feeding on the ground by hop and peck;
- 5) leaf gleaning (picking items from leaves).

We assessed these variables in an instantaneous sampling. In most cases it was impossible to assess if a bird succeeded in its prey capture (see also MORENO, 1984). Perch height, distances to prey and distance to the next perch were roughly estimated in meters, sometimes supported by the use of a ruler (MORENO, 1984). We calculated the means of perch height, prey distance and distance to the next perch. Number of aerial sallying and of perch-and-pounce were standardised on 60 s. Observations lasted between 30 s and 627 s (mean \pm se: 162 s \pm 11). We observed 117 foraging Cyprus Wheatears, 94 males and 23 females. Most data were reported for all 117 individuals, however some variables could not be obtained for some individuals and sample size differs in distance to prey (N = 111) and distance to the next perch (N = 109).

Weather variables

We assessed wind speed by using the Beaufort scale (mean \pm SE: 1.1 \pm 0.1; range 0–3.5), cloud cover in % (35 \pm 3, range 0–100 %), actual precipitation (yes/no; 112 observations without and 5 with rain), and temperature (20 \pm 0.3, range 10 °C to 28 °C).

Results

Different weather conditions as abiotic factors influenced the foraging behaviour of the Cyprus Wheatear in an amply manner which changed dependently on temperature, wind strength, cloud cover and precipitation. Time of day had only a low influence on foraging behaviour. Furthermore, we found sexual differences in the foraging behaviour.

Influence of weather conditions

Temperature, cloud cover and precipitation influenced perch height, distance to prey, numbers of aerial sallying/minute and perch and pounce/minute. A high cloud cover resulted in significant lower perches (Table 1) and lower distances to prey. Aerial sallying also declined with an increasing cloud cover, while the number of perch-pounce hunting was significantly higher during cloudy weather conditions. With higher air temperature aerial sallying increased and perch-pounce hunting decreased. Also, perch height and distance-to-prey showed a positive correlation with temperature (see Table 1). In contrast to temperature, wind had an inverse influence on the hunting behaviour of the Cyprus Wheatear. Aerial sallying was negatively and the perch-pounce strategy was positively related to wind speed (see Table 1). Finally we found a significant influence of the precipitation on the hunting behaviour. Like cloud cover, the precipitation influenced the perch height, the distance to prey, aerial sallying and the perch-pounce hunting (see Table 2).

Sexual differences

Clear differences between the sexes in the use of hop-and-peck as foraging technique and the perch height could be observed ($\chi^2_1 = 9.27$, $p = 0.002$). Males often used their hunting perch simultaneously as song post, usually during aerial sallying. Perches also used as song posts were higher than perches used for hunting only. Nevertheless, sex differences remained significant when excluding song posts and considering only perches used for hunting ($Z = -1.99$, $p = 0.046$; 2.6 ± 0.4 m vs. 1.3 ± 0.2 m).

Discussion

We observed more males than females during our study. This may arise because in Cyprus Wheatears, females seem to do all/most incubating alone (see HARRISON, 2008; but quantitative evidence is lacking: ASHTON-JOHNSON, 1961¹). Our study suggests that there is a strong influence of weather conditions, as crucial abiotic factor, on the foraging behaviour of an insectivorous bird species, the Cyprus Wheatear. Furthermore, we provide data that hunting strategies differ between the sexes in this species. Time of day had only a low influence on foraging behaviour. This is unusual because similar small turdid species, such as the Black Redstart *Phoenicurus ochruros* show differences in diurnal and seasonal rhythms (NICOLAI, 1992). However, this may be clarified in more complex studies. Similar to other studies, we suppose that an increase of foraging at higher temperatures and during less windy conditions reflects the prey-availability (HOLMES *et al.*, 1978; SCHAUB, 1996; LOW *et al.*, 2008).

Weather conditions

We found that during cloudy weather conditions and precipitation the Cyprus Wheatear significantly preferred the perch-pounce technique from low perches with short distances to prey. In contrast, MURPHY (1987) found perch heights unrelated to wind speed, air temperature and cloud cover, which is counter-intuitive and may be a result of low sample size in that study ($N = 40$). One aspect responsible for this may be the visual range (KILTIE, 2000). These authors showed that eye size and thus the visual acuity of a bird species depends on its body size. As a small insectivorous bird, the range of vision for *Oenanthe cypriaca* may be limited in general – especially during cloudy or rainy conditions from a high perch searching on the ground. So it is more effective to hunt from lower perches where the view is best adapted under these weather conditions. Although consequently the area which the bird can scan from a low perch is small, it is visible without barriers. Hence the distance to prey is small and the perch-pounce as foraging technique more effective during cloudy and rainy weather conditions.

The Cyprus Wheatear mainly feeds on arthropods (PANOV, 2005), which can be found on the ground or – flying – in the air. Since arthropods are ectothermic their activity depends mainly on the temperature (AVERY & KREBS, 1984). The Cyprus Wheatear adapts its foraging technique to the temperature. Flying arthropods are more abundant during higher temperatures (SCHAUB, 1996). So it is more effective under these conditions to use aerial sallying to increase the hunting

1 In *O. pleschanka*, only females breed, but according to ASHTON-JOHNSON (1961) in *O. cypriaca* both sexes breed, but quantitative data are lacking and perhaps females breed a higher amount of time.

Tab. 1. Correlations between weather conditions (wind speed, air temperature, cloud cover) and foraging behaviour in Cyprus Wheatears. Non-parametric Spearman rho was used. * indicates $p \leq 0.05$, ** $p \leq 0.01$.

	Temperature	Wind speed	Cloud cover	Time of day
MEAN perch height	.298**	-.149	-.358**	.060
MEAN distance to prey	.196*	-.142	-.255**	-.039
MEAN distance to next perch	.069	-.035	-.084	-.025
MEAN aerial sallying / minute	.512**	-.460**	-.534**	-.114
MEAN perch-pounce/ minute	-.259**	.303**	.315**	.200*

Tab. 2. Influence of precipitation on foraging behaviour of the Cyprus Wheatear. 0=days without precipitation (N=115 observations), 1=days with precipitation (N=5 observations).

		Mean	SE	Z	P
MEAN perch height	0	2.9	.3	-2.594	.009
	1	.7	.4		
MEAN distance to prey	0	2.6	.2	-2.489	.013
	1	.8	.4		
MEAN distance to next perch	0	7.6	1.0	-.906	.365
	1	2.8	.9		
MEAN aerial sallying / minute	0	1.1	.1	-2.322	.020

Tab. 3. Sexual differences in foraging behaviour of the Cyprus Wheatear.

		N	Mean	SE	Z	p
MEAN perch height	♂	94	3.2	.3	-3.330	.001
	♀	23	1.3	.2		
MEAN distance to prey	♂	88	2.5	.2	-.139	.890
	♀	23	2.4	.4		
MEAN distance to next perch	♂	88	7.7	1.2	-.512	.609
	♀	21	6.1	1.3		
MEAN aerial sallying / minute	♂	94	1.1	.1	-.390	.696
	♀	23	1.0	.3		
MEAN perch-pounce/ minute	♂	94	1.6	.2	-1.022	.307
	♀	23	1.8	.3		

success. Usually, time of day and temperature are inevitable linked (Low *et al.*, 2008), but our data strongly suggest that it is the temperature rather than time of day. Time of day may be unrelated to foraging because air temperatures are rather warm on Cyprus, compared e.g. to studies in Central or Northern Europe (KNEIS & LAUCH, 1983).

In this context, also the wind speed plays an important role in the foraging behaviour of the Cyprus Wheatear. Because of their very low weight, the abundance especially of flying arthropods seems strongly influenced by wind (despite contrary evidence in SCHAUB, 1996). Logically, under windy weather conditions there seem to be more ground arthropods than flying arthropods. Hence, it is more effective to forage on arthropods in the air with aerial sallying at low wind speed. Vice versa, during higher wind speed, it

is more effective to forage on ground arthropods by perch-pounce technique. However, aerial sallying may be also more energetically demanding during windy conditions.

Sexual dimorphism

Although the sexual dimorphism is very low in the Cyprus Wheatear (CHRISTENSEN, 1974), we found sexual differences in the hunting behaviour. The perch heights and hop-and-pecks as foraging techniques differed between the sexes. Assuming that males in general use more often high perches and aerial sallying to forage, females, however, are more likely to be found on the ground or at lower perches. The fact that males use perches for both, singing and hunting

at nearly the same time may explain these differences. Sometimes singing is interrupted just a few seconds to catch flying arthropods in the air (personal observations). Since male Cyprus Wheatears use high perches for singing it does not matter if they use this perch for foraging too, because they are exposed anyway. Nevertheless, when considering only perches used for hunting, males also preferred higher perches than females.

Differentiation in perch height may reduce intra-pair competition because males and females forage in different space and the distance to prey did not differ between the sexes. Furthermore, the sexual differences in the hunting behaviour of Cyprus Wheatears support the idea of specialised niches depending on the sex of a species, especially during periods with shared purpose such as the breeding season.

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References

- ASHTON-JOHNSON, J.F.R. (1961): Notes on the breeding birds of Cyprus. – *Oological Record*, **35**: 33–39.
- AVERY, M.I. & KREBS, J.R. (1984): Temperature and foraging success of great tits *Parus major* hunting for spiders. – *Ibis*, **126**: 33–38.
- BERGMANN, H.H. (1983): Some peculiarities of Cyprus bird voices. – *Cyprus Ornithology Society Report*, **8**: 41–54.
- CHRISTENSEN, S. (1974): Notes on the plumage of the female Cyprus Pied Wheatear *Oenanthe pleschanka cyprica*. – *Ornis Scandinavica*, **5**: 47–52.
- EAST, M. (1980): Sex differences and the effect of temperature on the foraging behaviour of Robins *Erithacus rubecula*. – *Ibis*, **122**: 517–520.
- FLINT, P. & STEWART, P. (1992): *The birds of Cyprus*. – British Ornithologist's Union: Tring.
- FÖRSCHLER, M.I. & RANDLER, C. (2009): A song analysis of the insular Cyprus Short-toed Treecreeper, *Certhia brachydactyla dorotheae*, supports its subspecies status (Aves: Passeriformes). – *Zoology of the Middle East*, **46**: 37–40.
- FÖRSCHLER, M.I., RANDLER, C., DIERSCHKE, J. & BAIRLEIN, F. (2010): Morphometric diagnostibility of Cyprus Wheatears *Oenanthe cyprica* and an unexpected occurrence on Helgoland Island. – *Bird study*, **57**: 396–400.
- FRANZREB, K.E. (1983): Intersexual habitat partitioning in yellow-rumped warblers during the breeding season. – *Wilson Bulletin*, **95**: 581–590.
- GRUBB, T.C.Jr. (1982): On sex-specific foraging behaviour in the white-breasted nuthatch. – *Journal of Field Ornithology*, **53**: 305–462.
- HARRISON, C., CASTELL P. & HOERSCHELMANN H. (2008): *Jungvögel, Eier und Nester der Vögel Europas, Nordafrikas und des Mittleren Ostens*. Aula: Wiebelsheim.
- HOLMES, R.T.; SHERRY T.W. & BENNETT, S.E. (1978): Diurnal and individual variability in the foraging behaviour of American Redstarts (*Setophaga ruticilla*). – *Oecologia*, **36**: 141–149.
- HURLBERT, S.H. (1984): Pseudo-replication and the design of ecological field experiments. – *Ecological Monographs*, **54**: 187–211.
- JONES, V.R. 2006. Comparative ecology of the endemic Cyprus Warbler and the congeneric Sardinian Warbler: implications of recent coexistence. Cambridge: PhD dissertation.
- KABOLI, M., ALIABADIAN, M., THEVENOT, M., GUILLAUME, C.P. & PRODON, R. (2006): Ecological segregation between Iranian wheatears. – *Zoology in the Middle East*, **39**: 41–58.
- KABOLI, M., ALIABADIAN, M., GUILLAUMET, A., ROSELAAR, C.S. & PRODON, R. (2007): Ecomorphology of the wheatears (genus *Oenanthe*). – *Ibis*, **149**: 792–805.
- KILTIE, R.A. (2000): Scaling of visual acuity with body size in mammals and birds. – *Functional Ecology*, **14**: 226–234.
- KNEIS, P. & LAUCH, M. (1983): Investigations on the foraging in the Wheatear *Oenanthe oenanthe* (Turridae). – *Zoologische Jahrbücher Physiologie*, **87**: 381–390.
- KRYSTOKOVÁ, M., EXNEROVÁ, A. & PORKERT J. (2006): Parental foraging strategies and feeding of nestlings in common redstarts *Phoenicurus phoenicurus*. – *Ornis Fennica*, **83**: 49–58.
- LEWIS, S., BENVENUTI, S., DALL'ANTONIA, L., GRIFFITHS, R., MONEY, L., SHERRAT, T.N., WANLES, S. & HAMER, K.C. (2002): Sex-specific foraging behaviour in a monomorphic seabird. – *Proceedings of the Royal Society London B: Biological Sciences*, **269**: 1687–1693.
- LOW, M., EGGERS, S., ARLT, D. & PÄRT, T. (2008): Daily patterns of nest visits are correlated with ambient temperature in the Northern Wheatear. – *Journal of Ornithology*, **149**: 515–519.
- MARTIN, P. & BATESON, P. (1993): *Measuring Behaviour. An introductory guide*. – Cambridge University Press, Cambridge.
- MORENO, J. (1984): Search strategies of wheatears (*Oenanthe oenanthe*) and stonechats (*Saxicola torquata*): adaptive variation in perch height, search time, sally distance and inter-perch move length. – *Journal of Animal Ecology*, **53**: 147–159.
- MURPHY, M.T. (1987): The impact of weather in kingbird foraging behavior. – *Condor*, **89**: 721–730.

- NICOLAI, B. (1992): Investigations of the food and the foraging of Black Redstart (*Phoenicurus ochruros*). – Ornithol. Jber. Mus. Heineanum, **10**: 75-105.
- PANOV, E.N. (2005): Wheatears of Palearctic. Ecology, Behaviour and Evolution of the Genus *Oenanthe*. – Pensoft Publishers: Sofia-Moskau.
- PASINELLI, G. (2000): Sexual dimorphism and foraging niche partitioning in the Middle Spotted Woodpecker *Dendrocopos medius*. – Ibis, **142**: 635–644.
- PECHACEK, P. (2006): Foraging behaviour of Eurasian three-toed Woodpeckers (*Picoides tridactylus alpinus*) in relation to sex and season in Germany – The Auk, **123**: 235–246.
- PETERS, W.D. & GRUBB, T.C.Jr. (1983): An experimental analysis of sex-specific foraging in the Downy Woodpecker *Picoides pubescens*. – Ecology, **64**: 1437–1443.
- RANDLER, C., TEICHMANN, C. & PENTZOLD, S. (2010): Breeding habitat preference and foraging of the Cyprus Wheatear *Oenanthe cypriaca* and niche partitioning in comparison with migrant *Oenanthe* species on Cyprus. – Journal of Ornithology, **151**: 113–121.
- RANDLER, C. (2010): Resource partitioning between the breeding migrant Cyprus Wheatear, *Oenanthe cypriaca*, and the passage migrant Spotted Flycatcher, *Muscicapa striata*, in Cyprus (Aves: Passeriformes). – Zoology in the Middle East, **49**: 33–38.
- SALEWSKI, V., BAIRLEIN, F. & LEISLER, B. (2003): Niche partitioning of two Palearctic passerine migrants with Afrotropical residents in their West African winter quarters. – Behavioural Ecology, **14**: 493–502.
- SANTOS, T. & SUÁREZ, F. (1983): The intersexual differentiation in the foraging behaviour of *Oenanthe hispanica* L. during the breeding season. – Acta Donana Vertebrata, **12**: 93–103.
- SCHAUB, M. (1996): Jagdverhalten und Zeitbudgets von Rotkopfwürgern *Lanius senator* in der Nordwestschweiz. – Journal of Ornithology, **137**: 213–227.
- SELANDER, R. K. (1966): Sexual dimorphism and differential niche utilization in birds. – Condor, **68**: 113–151.
- SLUYS, R. & van den BERG, M. (1982): On the specific status of the Cyprus Pied Wheatear *Oenanthe cypriaca*. – Ornis Scandinavica, **13**: 123–128.
- STENBERG, I. & HOGSTAD, O. (2004): Sexual dimorphism in relation to winter foraging in the white-backed woodpecker (*Dendrocopos leucotos*). – Journal of Ornithology, **145**: 321–326.