Original article

Foraging behaviour and diet in two sympatric shrike species during autumn migration across the Arabian Peninsula

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ABSTRACT

In situations of restricted food supply, the trophic niches of closely-related species of animals should be separate. For sit-and-wait hunters, such as shrikes, this is associated with competition for food and hunting sites. In the present study, the foraging behaviour of two shrike species – Red-tailed Shrike *Lanius phoenicuroides* and Red-backed Shrike *Lanius collurio* – was studied in a desert habitat in Oman. The field-work was carried out in September 2019, during the peak migration of these birds. Their behaviour was recorded in detail during 30-minute observation bouts. A General Linear Mixed Model with logit link function and binomial error variance was used to compare their behaviour. The type of perch and its height did not differ between them, but there were significant differences in their use of look-out posts only in the mean duration of a single perching event, which was more than twice as long in Red-backed Shrike. No differences in prey size were found between the species and hunting success (the ratio of successful attacks to all attacks) was similar in both (RtS-RbS: 46 vs. 61%). Dietary diversity was twice as great in Red-tailed Shrike as in Red-backed Shrike, but in general, their diets did not differ very much. Dietary overlap between the species at this level of prey identification was 92%. This absence of differences in some aspects of behaviour and diet may be due to the similarity of the two species, above all their same body size, and even the possibility of hybridization. If the species compared are so similar due to body size, behaviour and evolutionary relationship their food niches may overlap.
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1. Introduction

Studies of diet and niche overlap are crucial for understanding the co-occurrence of species with similar morphological and ecological features (Gonzalez-Solis et al., 1997; Garcia and Arroyo, 2005; Berzaghi et al., 2018; Pande et al., 2018). Closely related species of animals often partition resources such as space and food in ways that reduce competition, and they are expected to develop strategies of niche differentiation (Lack, 1970; Chesson and Huntly, 1997). On the other hand, it also happens that some individuals of one species use successfully settled individuals of a different species as a source of information indicating the location of high quality habitat (Hromada et al., 2008). Abundance of food can lead to a high degree of dietary overlap between two species, but in conditions of restricted access to food, dietary overlap is expected to decrease and interspecific competition to intensify (Wiens, 1989). Should the restrictions in food supply persist, however, the trophic niche may once again overlap (Wiens, 1989; Bell and Ford, 1990).

Species have to share a variety of resources like food or habitat while contending with pressure from other species. For example, Leisler et al. (1983) reported that migrant Pied Wheatear *Oenanthe pleschanka* forages the quickest by flying longer distances compared to resident species of wheatears. Species may also change their foraging sites somewhat in response to the appearance of other species using a similar foraging niche (Jedlicka et al., 2006). Shrikes wintering in southern Africa may compete with one another for food and foraging sites, and other species with a similar habitat and food preferences may find themselves in antagonistic relationships with them (Bruderer and Bruderer, 2008; Golawski and Kasprzykowski, 2018). Direct agonistic interactions between

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individuals should be suggestive of possible interspecific competitive situations (Leisler, 1992; Salewski et al., 2007). Larger body size should confer an advantage in interspecific agonistic encounters (Shelley et al., 2004; Garcia and Arroyo, 2005).

Resource partitioning, coexistence and competition in many bird species have been studied largely in their breeding areas (Alatalo et al., 1986; Kaboli et al., 2006; Orłowski and Karg, 2013). These studies suggest that interspecific agonistic behaviour is rare, probably because resources (including food) are abundant (Leisler, 1992; Salewski et al., 2003). However, this might not be the case on stopover sites, where migrants concentrate in bigger numbers (Salewski et al., 2007). In many respects, this is a time when any kind of competition could be important: populations are large following breeding, many individuals converge over a short period on certain types of site, and some species at some locations may have heightened energetic requirements for pre-migratory fattening (e.g. Bibby and Green, 1981; Ormerod, 1990).

We examined foraging behaviour and diet in two sympatric shrike species during autumn migration to determine how they might coexist and partition available resources. For this research, we chose two very similar species (Fuchs et al., 2019) – Red-backed Shrike *Lanius collurio* and Red-tailed Shrike *Lanius phoenicuroides* – which migrate across the Arabian Peninsula to their wintering grounds in Africa. We hypothesized that diet in both species might vary in two ways with respect to: (1) the occurrence of major food types, i.e. the most numerous prey taxa, (2) prey diversity and food niche overlap between these species. To test these hypotheses, we analysed the potential dietary overlap/segregation between them. We also expected that feeding behaviour in the two species could differ, i.e. in the choice of type and height of perches, hunting type and success, as well as the size and taxon of prey. No such study has yet been conducted on any shrikes during migration periods, although similar studies have been performed in wintering areas (Bruderer and Bruderer, 2008; Golawski and Kasprzykowski, 2018). Most of the few publications about shrikes from the Arabian Peninsula are short communications: they describe the migrations of several species of shrike providing only brief information about food (Meadows, 2010; Tøttrup et al., 2012; Cogălniceanu et al., 2015) and they discuss the importance of facial mask for foraging preferences and hunting success (Yosef et al., 2012).

2. Material and methods

2.1. Study species

Red-backed Shrike and Red-tailed Shrike are small passerine species migrating to wintering grounds in tropical Africa (Harris and Franklin, 2000). The Red-tailed Shrike (a species separated from Isabelline Shrike *Lanius isabellinus* a few years ago) breeds in south-west Asia and occasionally overwinters in Oman, whereas Red-backed Shrike breeds in Europe and western Asia and is seen in Oman only during passage. Red-backed Shrike migrates most intensively in September, while Red-tailed Shrike does so between September and November (Eriksen and Victor, 2013). The body dimensions of both species are very similar and often overlap (Harris and Franklin, 2000; Worfolk, 2000): bill length – 17–20 mm, wing length – 87–100 mm, tail length – 69–82 mm, body mass – ca 30 g (Harris and Franklin 2000; Worfolk, 2000). Both species are mainly insectivorous species, and their habit of storing of food is well-known (Yosef and Pinshow, 2005; Tryjanowski et al., 2003; Golawski, 2006; Morelli et al., 2016). Hybrids between these two species are also found (Panov, 2011), but in this study we analysed only unambiguous phenotypically individuals.

2.2. Study area

The study areas lay mainly along the coast of Oman, and the data were gathered at four sites (Fig. 1). The principal habitat was desert adjacent to the buildings with scattered single shrubs, mostly *Acacia* species. Each of the surveyed areas abounded in bushes of different heights. In most places, there were fences of varying heights, as well as heaps of dry branches. The first area, with an abundance of various species of trees and shrubs, was in the outskirts of the city of Salalah. The second one was around the Nafun settlement (Al Wusta Governorate), where there were single trees and shrubs along the ocean coast. The third area was around Shnt village (Ash Sharqiyah South Governorate), with low mangroves growing in parts of the area. The fourth site was on Masirah Island, where acacia bushes were dominant. We did not find any shrikes between Salalah and Nafun (that is, a distance of ca 700 km along the ocean coast). The mean daily temperature in September in Salalah is ca. 27 °C, while on Masirah Island it is ca. 30 °C; total rainfall does not exceed 10 mm in both locations (https://en.tutiempo.net/climate).

2.3. Data collection

The fieldwork was carried out in September 2019, during the migration period of Red-tailed Shrike and Red-backed Shrike. Shrikes were searched for while driving along local roads. The fieldwork was carried out only on sunny days between 10:00 and 16:00 hrs local time. This covers a good part of the time when shrikes are actively hunting (Bruderer and Bruderer, 2008). The observers used 10x42 binoculars and 25-60x80 telescopes to watch the birds and to determine the size and taxon of prey, and a dictaphone to describe the shrikes' behaviour. Immediately after the observations, the area was checked for larders set up by the shrikes, because it is known that shrikes create them while migrating across the Arabian Peninsula (Meadows, 2010; Cogălniceanu et al., 2015). A total of 19 Red-backed Shrikes and 54 Red-tailed Shrikes were chosen to record, in places where there was relatively high heterogeneity of habitats. All the Red-backed Shrikes were found in proximity to the Red-tailed Shrikes; sometimes both species were perching on the same bush. The following foraging parameters were recorded: (1) height of all structures used for perching, (2) perch type (fences, bushes, heap of dry branches), (3) duration of perching, (4) hunting type (perch-to-ground, perch-to-air, surface gleaning of plants), (5) hunting success (successful or unsuccessful attack), (6) size and taxon of prey. The victims found in 16 larders (only in Salalah region) were measured and photographed.

Perch (look-out post) heights were measured with a tape measure after a bird had been observed. Because the birds were
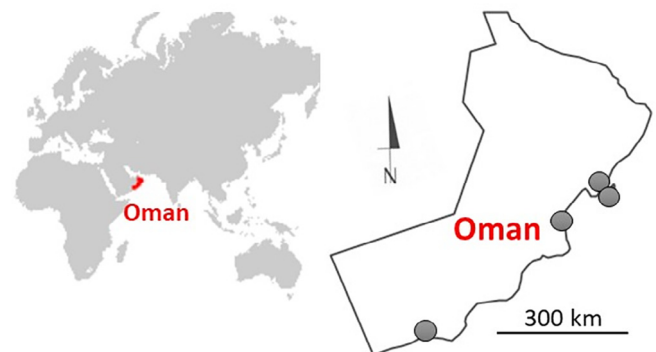

Fig. 1. Locations of the study sites (grey dots) in Oman.

not very mobile, it was easy to remember where they were during recording. A particular bird was observed for a maximum of 30 min unless it disappeared earlier, but for no less than five minutes (av. = 22 min, SE = 1.2, n = 73 birds). The mean duration of an observation session was 26.8 min. (SE = 2.3, n = 19) for the Red-backed Shrike, and 20.6 min. (SE = 1.4, n = 54) for the Red-backed Shrike. Overall, the observations lasted 1620 min.

Perching times were measured between two movements of a bird. The attack was deemed successful if the bird returned with a prey item in its bill. In most cases, the shrikes caught their prey and carried it back to the perch from which they had taken off, or close by. Prey size was assessed relative to the length of a shrike's beak, which is standard practice (Devereux et al. 2000). The mean beak length in both species is 18.5 mm (Worfolk, 2000), so any differences in prey size estimated with respect to the beak length of either of the species should thus be negligible. In our later analyses, the size of the victims was calculated as the proportion of the beak length × 18.5 mm. The taxonomic status of prey items could be determined in practice only for larger ones, and was limited to the order level. The victims in the larders were measured with a ruler accurate to 1 mm, and specialists were consulted in order to confirm their identities (based on photographs).

We planned to determine the abundance of potential prey in the area of shrike observations based on visual identification while searching along suitable transects. This method of assessing the faunal richness has frequently been used in studies of invertebrates, including the orders most commonly found in the diet of shrikes (Schulze et al., 2004; Schirmel et al., 2010). After five surveys, however, we gave up because we had failed to find any animal that might be a potential prey item of the shrikes; such items must therefore have been very rare.

2.4. Qualitative estimators of diet

Total identified prey items (combined data from observations and larders) were used to calculate diversity and niche overlap indices. Trophic diversity was calculated using the Shannon–Weaver index: H = −∑ pi * log pi, where pi = Xi/X, and Xi is the number of prey items taken from class i; X is the total number of prey items. Diet similarity between the two species of shrikes was evaluated using Pianka's index: Ov = ∑ $p_i q_i$ / (∑ p_i^2 * ∑ q_i^2)$^{1/2}$, where p_i and q_i are the frequency of occurrence of prey category i in the diets of the two species (Pianka, 1973). Pianka's index varies between 0 (total separation) and 1 (total overlap); values > 0.60 indicate overlap between species (Orłowski and Karg, 2013).

2.5. Statistics

A General Linear Mixed Model (GLMM) with logit link function and binomial error variance was used to compare the species' behaviour. The dependent variable was the species pair being compared (binomial variable: 0 – Red-backed Shrike, 1 – Red-tailed Shrike). The height of all the perching sites, type of perching site and duration of perching were treated as fixed effects; bird-ID (according to the order of observed birds) was a random factor. In addition, the χ^2 test (applying the Yates continuity correction when necessary) was used to compare hunting success, i.e. the ratio of successful attacks to all attacks, between the shrike species, and the hunting success of each species with respect to hunting type. The difference in the size of victims between the shrike species was calculated using Student's t-test. Statistical analyses were performed in SPSS v.21.0 (IBM Corp., 2012); $P < 0.05$ was considered statistically significant.

3. Results

3.1. Foraging behaviour

Red-backed Shrike most often perched on bushes (67.1%), less often on heaps of dry branches (28.6%) and the least frequently on fences (4.3%, n = 70). The mean perch height was 172.6 cm (SE = 14.1, Range 50–600 cm), and the mean perching time was 436.9 secs. (SE = 58.6, Range 1–1800). Red-tailed Shrike also most often used bushes as look-out posts (63.3%,), thereafter heaps of dry branches (19.3%) and fences (17.4%, n = 305). The mean perch height was 202.0 cm (SE = 8.7, Range 20–800 cm), and the mean perching time was 195.2 secs (SE = 14.0, Range 1–1800). There were significant differences between Red-tailed Shrike and Red-backed Shrike in their use of look-out posts only with respect to the mean time of a single perching event (GLMM, $F_{1,370}$ = 3.99, P = 0.046), which was more than twice as long in Red-backed Shrike. The type of look-out post and the perch height did not differ significantly between the two species (GLMM, P > 0.050 in both cases, Table 1). We observed no instance of very aggressive behaviour: only on two occasions did we see a Red-backed Shrike being gently chased off the perches by a Red-tailed Shrike.

3.2. Hunting success, prey size and taxonomic composition of prey

Hunting success was 45.7% (n = 115) in Red-tailed Shrike and 60.7% (n = 26) in Red-backed Shrike. These results did not differ statistically (Yates χ^2 = 1.48, df = 1, P = 0.224). Red-tailed Shrike attacked successfully every 21 min, Red-backed Shrike every 32 min. There were statistically significant differences between hunting success on the ground and in the air (Yates χ^2 = 5.62, df = 1, P = 0.018) in Red-backed Shrike, but in Red-tailed Shrike there were no significant differences in hunting success on the three types of site (χ^2 = 3.74, df = 2, P = 0.154, Fig. 2).

The average length of victims was 27.4 mm (SE = 3.3, Range 7–56 mm, n = 20) in Red-backed Shrike and 27.0 mm (SE = 2.3, Range 4–82 mm, n = 58) in Red-tailed Shrike. The largest victims were odonata and reptile. There were no significant differences as regards prey size between the two shrike species (t-test, t_{76} = 0.10, P = 0.922).

Orthopterans were clearly predominant in the diet in both species (Table 2). The victims included: *Ruspolia* spp. (5 individuals), *Schistocerca gregaria* (2), found in the larders of both shrikes, and *Heteracris* sp. (1) found in the larder of Red-tailed Shrike. Besides orthopterans, we also found Coleoptera, Scarabaeidae (3 indiv., in both shrikes) and one odonate (*Anax parthenope*) in the larder of a Red-tailed Shrike (Table 2).

3.3. Dietary diversity and overlap

Dietary diversity was twice as great in Red-tailed Shrike as in Red-backed Shrike, but the diet was generally not much differentiated (Table 2). Dietary overlap between the species at this level of prey identification was 92% (Table 2), a very high figure.

Table 1

Binomial generalized linear mixed models comparing perching site, perch height and perching time between Red-tailed Shrike *Lanius phoenicuroides* and Red-backed Shrike *Lanius collurio* in Oman. Statistically significant results are shown in bold.

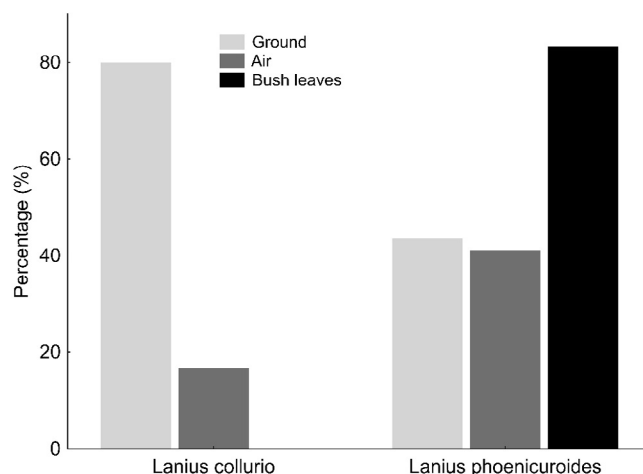| Variable	Estimate	SE	t-test	P
Perching site: bush	0.137	1.021	0.13	0.894
fence	1.302	1.556	0.84	0.403
heap of branches	0.000			
Perching height	0.001	0.003	0.26	0.798
Perching time	**−0.002**	**0.001**	**−1.99**	**0.046**

Fig. 2. Hunting success (%) with respect to the type of hunting sites in Red-backed Shrike *Lanius collurio* (n = 26) and Red-tailed Shrike *Lanius phoenicuroides* (n = 115).

4. Discussion

Our research did not show that the diets of Red-tailed Shrike and Red-backed Shrike differ and they contained the same food types with the most numerous prey taxa of orthopterans. In both shrike species, prey diversity and food niche overlapped strongly as well as feeding behaviour. If the analysed species are so similar due to body size, behaviour, evolutionary relationship and additionally food supplies are very limited, their food niches may overlap. This is the most important finding of this work. Earlier studies described that when foraging resources become less abundant, diet overlap is expected to decrease (Wiens, 1989; Gonzalez-Solis et al., 1997).

Shrikes are highly opportunistic feeders, preying on the most easily available victims (Harris and Franklin, 2000). Our data indicate that the hunting behaviours of Red-tailed Shrike and Red-backed Shrike were similar. They used different kind of perches, most often bushes, in similar proportions. Of course, the use of a particular type of perch depended on its availability (Morelli et al., 2016; Golawski and Kasprzykowski, 2018), so this result may simply be due to the predominance of bushes in the study area. The mean height of Red-backed Shrike perches appeared to be about 170 cm, and just a little more for Red-tailed Shrike. Perches at such a height should represent a good compromise between the possibility of detecting prey and the distance to be covered in order to capture it (Morelli et al., 2016), so this height was very similar in both shrikes. Only the mean duration of a single perching event differed: Red-backed Shrike was much less mobile than Red-tailed Shrike. During some observations, Red-backed Shrike did not move at all from its perch for half an hour. By comparison, the hunting frequency of the same species was > 20 times/hour in breeding areas in Switzerland (Bruderer and Bruderer, 2008), and ca 10 times/hour in eastern Poland (author's data). Perhaps the Red-backed Shrikes were more tired, because its breeding areas were farther away than those of the Red-tailed Shrikes. However, this was unrelated to the achieved hunting success, which was similar in both species. A hunting success of 60% is typical for Red-backed Shrike during the breeding season in Europe (Morelli et al., 2016), as well as in its wintering areas (Golawski and Kasprzykowski, 2018). Unfortunately, no such data are available for the Red-tailed Shrike. The Red-backed Shrike was evidently more successful hunting on the ground than in the air, but the small sample size was insufficient for a meaningful interpretation of this observation.

Dietary diversity was similar in Red-tailed Shrike and Red-backed Shrike, given the level of taxonomic precision used in this study, and trophic overlap between the species was very high (92%). The more precisely identified victims in the shrike larders (compared to the victims less precisely identified (order level) during observations) showed that the diet of both species was very similar. There is substantial food overlap between the two species when particular prey items are exceptionally abundant, while niche overlap decreases with falling food abundance (Wiens, 1989). The potential abundance of prey in the study area was probably very low: this was confirmed by the type of prey observed on Masirah Island, where birds even caught flies (the insects looked like *Musca* sp.). In eastern and southern Europe, where food is plentiful, Red-backed Shrikes completely ignore such insects (Golawski, 2006; Morelli et al., 2016). Hence, the considerable dietary overlap in these two shrike species in Oman is probably due to the limited availability of food, where the most numerous items are orthopterans.

Both shrikes have the same body size, and aggressive behaviour is probably rare – our data confirm this. Red-backed and Red-tailed shrikes are closely related to each other (Zhang et al., 2007), and some authors argue that the two species are in fact one single species (Cheng, 2000). Indeed, hybrid collurio × phoenicuroides birds are fairly common in eastern Kazakhstan (Kryukov, 1995, Panov, 2011). We, too, saw such a hybrid (male) in Oman, but we did not include it in the analyses.

5. Conclusion

The absence of differences in most of the feeding behaviour parameters may be due to the great similarity between the two species; above all, they are of the same body size. The prey composition was also very similar between the two shrikes, and trophic overlap was very high. These results do not confirm the hypothesis that when access to food is poor, dietary overlap is expected to

Table 2

Comparative data on the diet of two species of shrikes. Results are expressed as the number of prey items counted during observations of shrike hunting and prey items found in larders. H index = Shannon diversity index; Diet overlap = Pianka's index of niche overlap. Indices calculated with total identified prey (without the category "Invertebrata").

Taxon	*Lanius collurio*			*Lanius phoenicuroides*		
	Observations	Larders	Total	Observations	Larders	Total
Reptilia (lizard)	–	–	–	1	–	1
Coleoptera	2	1	3	1	2	3
Diptera	–	–	–	4	–	4
Hymenoptera	1	–	1	3	–	3
Lepidoptera	1	–	1	1	–	1
Odonata	2	–	2	4	1	5
Orthoptera	3	3	6	16	9	25
Invertebrata, not recognized	8	–	8	17	–	17
Total	17	4	21	47	12	59
H index		0.19			0.40	
Diet overlap	0.92					

decrease; we believe this is precisely because the body size of the two species is the same. However, it must be clearly stated that this study is based on a relatively short period of observations and a correspondingly small sample size, especially of identified shrike victims. Nonetheless, it may serve as a stimulus for further research.

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Authors' contributions

All authors conceived and designed the study. AG, ZK collected field data. AG performed statistical analyses and wrote parts of the manuscript (methods, results). ZK, TSS wrote parts of manuscript and gave comments on the manuscript. All authors read and approved the final manuscript.

The work has not been published previously, - it is not under consideration for publication elsewhere, - is approved by all authors, - if accepted, it will not be published elsewhere in the same form, in English or in any other language, including electronically without the written consent of the copyrightholder.

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