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TEMPORAL AND SPATIAL DIETARY VARIATION OF AMUR FALCONS (*FALCO AMURENSIS*) IN THEIR SOUTH AFRICAN NONBREEDING RANGE

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ABSTRACT.—We studied the spatial and temporal dietary patterns of the Amur Falcon (*Falco amurensis*), a nonbreeding Palearctic migrant to South Africa, by collecting regurgitated pellets at two large colonial roost sites, i.e., Middelburg and Newcastle, over 11 equal sampling periods during December 2012 to March 2013. We dried the pellets to constant mass and classified the prey items to the lowest taxonomic level possible. Amur Falcons fed mainly on invertebrates (seven orders), and occasionally on vertebrates (three orders). The five most abundant prey taxa (pooled for both sites) were: Coleoptera, Orthoptera, Isoptera, Solifugae, and Hymenoptera. Lepidoptera, Hemiptera, Passeriformes, Rodentia, and Soricomorpha were consumed almost 20 times less frequently. Isoptera, Hymenoptera, Lepidoptera, and Rodentia were consumed significantly more frequently at Middelburg, while Orthoptera and Solifugae were consumed more frequently at Newcastle. The consumption of Coleoptera did not differ significantly between sites but decreased through the season, being most important when falcons arrived in South Africa in December. Consumption of Orthoptera increased through the season and was greatest prior to migration. The percentages of Isoptera and Hymenoptera in the diet peaked at different periods, likely the result of prey population irruptions. Diet similarity of sample periods between sites ranged from 33.3–100% (mean = 69.5%), and within-site similarity among sample periods ranged from 50–100% (mean = 75.6%) and 37.5–100% (mean = 65.9%) for Newcastle and Middelburg, respectively. This study highlights the variable importance of specific prey taxa, predominantly invertebrates, for Amur Falcons during the overwintering period in South Africa.

KEY WORDS: *Amur Falcon; Falco amurensis; diet composition; land transformation; regurgitated pellets; invertebrates.*

VARIACIÓN TEMPORAL Y ESPACIAL DE LA DIETA DE *FALCO AMURENSIS* EN SU ÁREA NO REPRODUCTIVA DE SUDÁFRICA

RESUMEN.—Estudiamos los patrones temporales y espaciales de la dieta de *Falco amurensis*, un ave Paleártica que migra en la época no reproductora hasta Sudáfrica, mediante la recolección de egagrópilas en dos grandes dormitorios coloniales, i.e., Middelburg y Newcastle, durante 11 periodos iguales de muestreo desde diciembre de 2012 hasta marzo de 2013. Secamos las egagrópilas hasta conseguir un peso constante y clasificamos los ítems de presa al nivel taxonómico más bajo posible. *F. amurensis* se alimentó principalmente de invertebrados (siete órdenes) y ocasionalmente de vertebrados (tres órdenes). Los cinco taxa de presa más abundantes (combinando ambos sitios) fueron: Coleoptera, Orthoptera, Isoptera, Solifugae e Hymenoptera. Lepidoptera, Hemiptera, Passeriformes, Rodentia, y Soricomorpha fueron consumidos con una frecuencia casi 20 veces menor. Isoptera, Hymenoptera, Lepidoptera y Rodentia fueron consumidos significativamente con más frecuencia en Middelburg, mientras que Orthoptera y Solifugae fueron consumidos más frecuentemente en Newcastle. El consumo de Coleoptera no difirió significativamente entre los sitios, pero disminuyó a lo largo de la temporada, siendo más importante cuando los halcones llegaron a Sudáfrica en diciembre. El consumo de Orthoptera aumentó a lo largo de la temporada y fue mayor en el periodo previo a la migración. Los porcentajes de Isoptera e Hymenoptera en la dieta tuvieron su pico máximo en diferentes periodos, probablemente como resultado de irrupciones de las poblaciones de presas. La similitud de la dieta durante los periodos de muestreo entre los sitios osciló ente el 33.3–100% (media = 69.5%) y la similitud dentro de los sitios entre periodos de muestreo varió

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entre el 50–100% (media = 75.6%) y 37.5–100% (media = 65.9%) para Newcastle y Middelburg, respectivamente. Este estudio subraya la variación en la importancia de las distintas presas, predominantemente invertebrados, para *F. amurensis* durante el periodo invernal en Sudáfrica.

[Traducción del equipo editorial]

Understanding the feeding biology of migratory raptors in their nonbreeding range is important for their conservation (Siegfried and Skead 1971, Marti et al. 1987, Korb and Salewski 2000, Rojas and Stappung 2004). Raptors provide important ecosystem services but are sensitive to human-induced land transformation such as habitat loss (Newton 1979, Donazar et al. 1993, McCann 1994, Anderson et al. 1999, Sekercioglu 2012), agricultural transformation (Shrubb 1980, Biber 1990, Goriup and Batten 1990, Donazar et al. 1993, Anderson et al. 1999), and overgrazing (Anderson et al. 1999, Herremans and Herremans-Tonnoeyr 2000). These factors may affect the availability of roost sites, hunting grounds, and prey species abundance and diversity (Shrubb 1980, Buij et al. 2013). The application of pesticides can also cause declines in raptor populations (Cramp and Simmons 1980), either directly through consumption of poisoned prey (Biber 1990, Keith and Bruggers 1998) or indirectly through declines in prey abundance (Biber 1990, McCann 1994, Keith and Bruggers 1998).

Despite numerous anthropogenic threats, many raptor species continue to persist in human-altered landscapes. However, in some instances, such as the mass harvesting of Amur Falcons (*Falco amurensis*) at a migratory stopover site in India (Conservation India 2012), there may be increased threats to the long-term survival and conservation of the species. In 2012, when the harvesting was first identified, an estimated 120,000–140,000 birds were slaughtered each year (Conservation India 2015). Highlighting the plight of these birds resulted in the cessation of killings in Nagaland, although reports suggested that hunting continued in other areas, e.g. Assam and Manipur (Conservation India 2014). While conservation efforts continue, the effects of a reduced Amur Falcon population might, in turn, be predicted to cause cascade effects in both the breeding and nonbreeding grounds (Bouwman et al. 2012), especially with respect to invertebrate and pest population explosions. Bouwman et al. (2012) estimated that a single Amur Falcon consumes approximately 15 g of invertebrates daily, resulting in an annual reduction of approximately 1800

metric tons of invertebrates by southern African Amur Falcons.

Amur Falcons are small, sexually dichromatic falcons, with males averaging 135 g (range 97–155 g) and females averaging 148 g (range 111–188 g; Jenkins 2005). They breed in eastern Siberia, Mongolia, and northern China from June to October (Schäfer 2003, Jenkins 2005). In November, the species migrates south to the grasslands and open savannas of southern Africa (Maclean 1993, Schäfer 2003, Jenkins 2005, Chittenden 2007), which have abundant invertebrate prey during the austral summer (Siegfried and Skead 1971, McCann 1994, Kok et al. 2000). In South Africa, they roost communally, often in urban environments where there are large, often exotic, trees such as *Eucalyptus* spp. or *Pinus* spp. (Jenkins 2005). Although food availability may not be the limiting factor influencing Amur Falcon populations, knowledge of diet is important for conservation (Reynolds et al. 1992, Kopij 2002, 2009).

Falcons and kestrels consume mainly vertebrates, with supplemental invertebrates, on their breeding grounds (Franco and Andrada 1977, Schäfer 2003, Geng et al. 2009), but tend to alter their diet while at their nonbreeding sites, eating mainly invertebrates (McCann 1994, Kopij 1998, Anderson et al. 1999, Kok et al. 2000, Kopij 2002, 2005, 2007, 2009, Pietersen and Symes 2010, Bouwman et al. 2012). Specifically, dietary studies of Amur Falcons on their nonbreeding grounds in South Africa suggest that they exhibit weak interspecific competition with Lesser Kestrels (*Falco naumanni*) where they co-occur (Newton 1979, Ristow 2004, Kopij 2009, Pietersen and Symes 2010). In addition, Amur Falcons are important predators of agricultural pests (Kopij 2009, Pietersen and Symes 2010, Bouwman et al. 2012).

The aim of our study was to investigate the diet of Amur Falcons on their winter nonbreeding grounds in South Africa. We attempted to answer the following questions: (1) Does the diet of Amur Falcons vary between two different sites in the grassland biome of South Africa, (2) does the diet of Amur Falcons vary during the period in which they are present in South Africa and are there specific prey taxa which are important in their

Table 1. Ecological and climatic comparison between the two roost sites where Amur Falcon (*Falco amurensis*) pellets were collected. Data taken from sources as indicated in the footnotes.

DESCRIPTOR	MIDDELBURG	NEWCASTLE
Roost trees	<i>Eucalyptus</i> spp.	<i>Pinus</i> spp.
Latitude (°S)	25.772942	27.742556
Longitude (°E)	26.463519	29.936986
Vegetation type ^a	Rand Highveld grassland	Northern KwaZulu-Natal moist grassland
Dominant grass species ^a	<i>Themeda</i> spp., <i>Eragrostis</i> spp., <i>Heteropogon</i> spp., <i>Elyonurus</i> spp.	<i>Themeda triandra</i> , <i>Hyparrhenia hirta</i>
Land transformation (%) ^a	50	25
Land transformation type ^a	Agriculture (maize), afforestation, dams	Agriculture (livestock), afforestation
Mean annual temperature (°C) ^b	15.8	16.2
Annual precipitation (mm) ^b	654	840
Precipitation during study months (mm) ^c	324	317
Altitude (masl) ^a	1480	1200
Falcon numbers ^d	Mean 2890 (16 yr) (range 700– 14,000)	Mean 18,806 (7 yr) ^e (range 8750– 36,400)

^a Mucina and Rutherford (2006).

^b SA Explorer (2013).

^c South African Weather Service (2013).

^d Migratory Kestrel Project (1995–2010 annual co-ordinated roost count).

^e Possibly the largest roost in South Africa.

nonbreeding grounds, and (3) if so, when are these taxa most important?

METHODS

Study Sites. The study was conducted during December 2012–March 2013, coinciding with the occurrence of Amur Falcons in the South African nonbreeding grounds. We found two large roosts in the grassland biome, namely Middelburg and Newcastle, 223 km apart. Middelburg was typically drier than Newcastle and had fewer overwintering falcons (Table 1).

Experimental Design and Protocol. We collected pellets every 5–11 d from beneath each roost. Small raptors usually regurgitate one to two pellets each morning (Bond 1936, Duke et al. 1976) comprising indigestible prey remains from the previous day's food (Duke et al. 1976, Yalden and Yalden 1985). We stored the pellets individually in brown paper bags marked with sampling locality and date. Pellets were presumed to be fresh, as precipitation would break apart and decompose any exposed pellets (J. Alexander unpubl. data). We collected only whole pellets to avoid any discrepancies during analyses. We walked beneath the roost trees collecting pellets until we had at least 15 pellets on each site visit; thus, not all pellets were collected. We dried pellets

at 50°C in a drying oven for one week, and separated each pellet by hand and analyzed each using a Motic ST-39 Series Binocular Stereo microscope at 20× magnification. We separated identifiable prey remains and classified them to order (Fattorini et al. 2001, Kopij 2009), and then to the lowest taxonomic level possible. We used field guides (Scholtz and Holme 1985, Picker et al. 2001) and reference collections to identify prey remains, based on the main identifying characteristics of insect orders and families. We identified vertebrate prey using reference collections, and photographed remains during sampling for consistent identification. We estimated the percentages of each taxa per pellet using a modification of the frequency of occurrence method used by Kopij (2009): the number of items of each taxon was divided by the total number of all items identified in that pellet. We averaged the percentages of each taxon per pellet to give a dietary percentage for each taxon per period. Although this method does not account for biomass and the underrepresentation of larger prey items, or the variable digestibility of different taxa (e.g., soft bodied versus hard-bodied organisms, which in turn would bias a biomass interpretation), it does at least allow for a relative comparison between periods within dietary

Table 2. Summary of 10–11-d sampling periods, collection date, and number of Amur Falcon (*Falco amurensis*) pellets (*n*) collected at Middelburg and Newcastle roosts during December 2012 to March 2013.

SAMPLE PERIOD	PERIOD	MIDDELBURG		NEWCASTLE	
		COLLECTION DATE	PELLETS (<i>n</i>)	COLLECTION DATE	PELLETS (<i>n</i>)
11–20 December 2012	DEC _{D2}	18 December 2012	11	17 December 2012	37
21–31 December 2012	DEC _{D3}	23, 31 December 2012	16, 18	24 December 2012	25
1–10 January 2013	JAN _{D1}	6 January 2013	17	7 January 2013	30
11–20 January 2013	JAN _{D2}	14 January 2013	18	14 January 2013	16
21–31 January 2013	JAN _{D3}	22, 30 January 2013	24, 20	21, 28 January 2013	30, 30
1–10 February 2013	FEB _{D1}	5 February 2013	18	4 February 2013	31
11–20 February 2013	FEB _{D2}	11, 17 February 2013	18, 25	11, 18 February 2013	31, 30
21–28 February 2013	FEB _{D3}	24 February 2013	44	25 February 2013	30
1–10 March 2013	MAR _{D1}	3 March 2013	26	4 March 2013	30
11–20 March 2013	MAR _{D2}	11, 18 March 2013	16, 41	11 March 2013	32
21–31 March 2013	MAR _{D3}	26, 31 March 2013	24, 25	25, 31 March 2013	32, 35
TOTAL	11	16	361	14	419

taxa (Frost 1977, Hyslop 1980, Morey et al. 2007). The size of prey items of Amur Falcons in their nonbreeding range probably does not differ by an order of magnitude, and because large prey items (vertebrates) are not well represented in the diet, a dietary assessment in this manner can be considered appropriate (Hyslop 1980; Morey et al. 2007).

The actual sampling days differed for Middelburg and Newcastle, so batches were allocated to 10-d and 11-d sample periods, facilitating the comparison between sites. This gave three 10–11-d periods each month (see also Kopij 2009; Table 2). From here on, we refer to the sampling periods in an abbreviated form such that MAR_{D3} = the third 10–11-d sampling period in March, etc.

Statistical Analyses. We performed all statistical analyses using R statistical programming (R Development Core Team 2013). We report mean values (\pm SD) unless otherwise indicated. As a Shapiro-Wilk’s test indicated that the data were not normally distributed, and given that the data were percentages, we used arcsine transformations to meet the requirements for normality. We used *t*-tests to investigate differences in taxon percentages between the two sites, ANOVA tests to determine whether there was a temporal change in diet through the nonbreeding season at each of the sites, and Tukey HSD tests to identify within-season differences. We performed Pearson correlations to analyze the relationships among prey taxa at each roost site. We performed a Jaccard cluster analysis using BioDiversity Professional (McAleece et al. 1997) to determine the dietary similarity among

sampling periods within and between the two study sites, and we used a *t*-test to determine whether the dietary similarity of the sample periods varied significantly between the sites.

RESULTS

Pellets Collected. We collected 361 pellets from Middelburg and 419 from Newcastle, a total of 780 pellets. We excluded pellets collected at Middelburg on 9 December 2012 due to the small number of pellets (*n* = 6) from only a few Amur Falcons that had arrived at the roost early. We collected an average of 37 ± 15 pellets at Middelburg and 39 ± 16 at Newcastle for each sampling period.

Diet. We identified seven invertebrate and three vertebrate orders from the pellets, with all prey taxa present in both the Middelburg and Newcastle pellets. Of the 10 orders recorded, 12 families and a further four sub-families were identified (Appendix 1). We identified two taxa to species level; namely *Odontotermes badius* (Isoptera) and *Heteronychus arator* (Coleoptera). The most abundant taxa by percentage of items found in both the Middelburg and Newcastle pellets were: Coleoptera (39.3%), Orthoptera (38.1%), Isoptera (7.9%), Solifugae (6.1%), and Hymenoptera (3.8%). These five invertebrate taxa made up 95.2% of the diet, whereas vertebrate prey composed <1% of the diet at both sites (Fig. 1). The percentage of invertebrate (*t* = 0.022, *df* = 6, *P* = 0.983) and vertebrate (*t* = 1.971, *df* = 2, *P* = 0.188) prey as a whole did not differ between sites, despite more vertebrate prey being consumed at Middelburg.

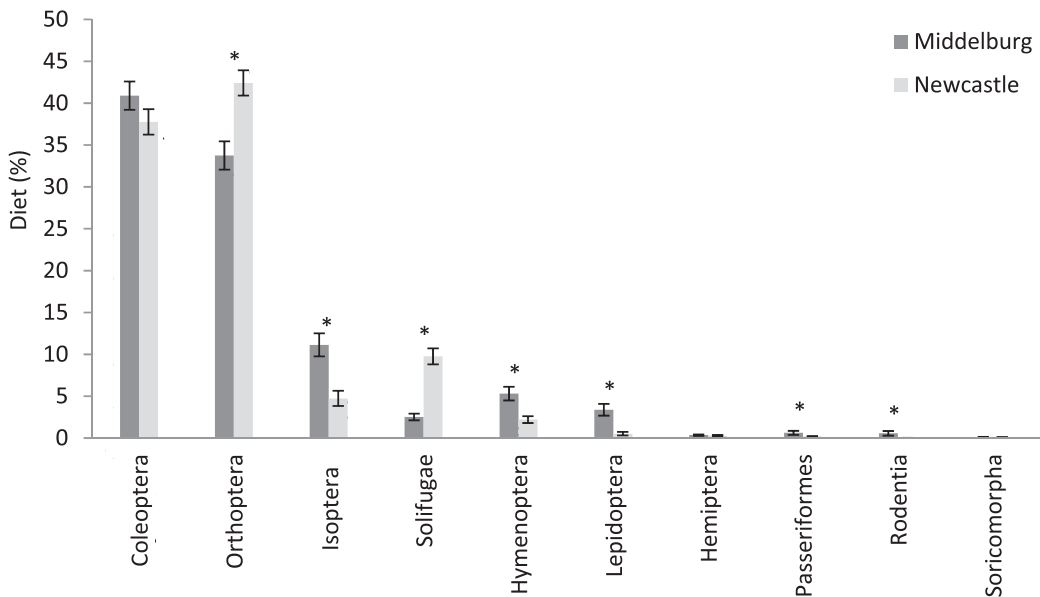


Figure 1. Percentage (mean % per sampling period \pm SE) of vertebrate and invertebrate prey orders recorded in the diet of Amur Falcons (*Falco amurensis*) from Middelburg and Newcastle. Significant difference in percentages of each taxon between sites indicated by * (*t*-Test: $P < 0.05$).

The five most abundant taxa in the diet of the Middelburg falcons were Coleoptera (40.9%), Orthoptera (33.7%), Isoptera (11.1%), Hymenoptera (5.3%), and Lepidoptera (3.4%), which together made up 94.4% of the diet (Fig. 1). Two additional invertebrate taxa were consumed in much smaller percentages: Solifugae (2.5%) and Hemiptera (0.4%). Vertebrate prey (identified from bone remains) comprising Passeriformes, Rodentia, and Soricomorpha contributed only 1.3% of the seasonal diet. At Newcastle, the most abundant prey items were Orthoptera (42.4%), Coleoptera (37.8%), Solifugae (9.8%), Isoptera (4.7%), and Hymenoptera (2.2%). These taxa together made up 96.7% of the diet. The additional invertebrate taxa Lepidoptera (0.5%) and Hemiptera (0.3%) contributed fractionally to the diet, while vertebrate taxa contributed <1%.

Diet comparison between and within sites. There was no significant difference in the percentage of Coleoptera consumed between the two sites ($t = 1.398$, $df = 779$, $P = 0.162$; Fig. 1, Appendix 2). The percentage of Coleoptera in the diet decreased significantly through the nonbreeding season at both Middelburg ($F = 10.950$, $df = 10$, $P < 0.001$) and Newcastle ($F = 2.228$, $df = 10$, $P = 0.015$), with a greater decrease at Middelburg than Newcastle

(Fig. 2a, Table 3). At Middelburg the percentage of Coleoptera in the diet for MAR_{D3} was significantly lower than that in $DEC_{D2, D3}$, $JAN_{D2, D3}$, and $FEB_{D1, D2}$ (TukeyHSD: $P < 0.05$).

Overall, Orthoptera percentages were significantly higher at Newcastle than at Middelburg throughout the nonbreeding season ($t = 3.871$, $df = 779$, $P < 0.001$; Fig. 1, Appendix 2). Orthoptera percentages increased significantly throughout the nonbreeding season at both Middelburg ($F = 10.710$, $df = 10$, $P < 0.001$) and Newcastle ($F = 7.529$, $df = 10$, $P < 0.001$; Fig. 2b, Table 3). Orthoptera percentages at Middelburg were significantly higher toward the end of the season (FEB_{D3} and $MAR_{D2, D3}$) compared to the start of the season ($DEC_{D2-FEB_{D2}}$). At Newcastle there was a significant peak during $JAN_{D3-FEB_{D2}}$, which was not significantly different from the end of the season (MAR_{D1-D3}). However, $JAN_{D3-FEB_{D2}}$ and $MAR_{D1, D3}$ Orthoptera percentages were higher than the beginning of the season (DEC_{D2} and JAN_{D2} ; Tukey HSD: $P < 0.05$).

The percentage of Isoptera in the diet was significantly higher at Newcastle than at Middelburg ($t = 4.006$, $df = 779$, $P < 0.001$; Fig. 1, Appendix 2). Isoptera percentages differed significantly throughout the season at Middelburg ($F = 14.640$, $df = 10$, $P < 0.001$) but not at Newcastle ($F = 1.443$, $df = 10$, P

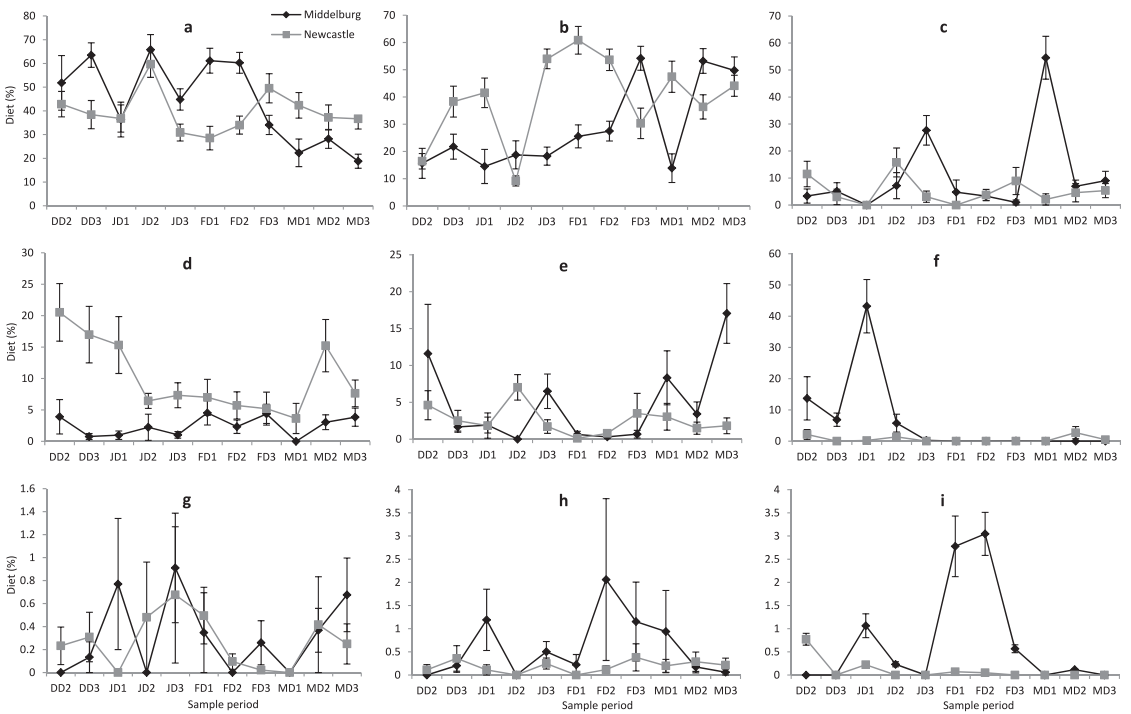


Figure 2. Amur Falcon (*Falco amurensis*) dietary percentages (mean % per sampling period \pm SE) of: (a) Coleoptera, (b) Orthoptera, (c) Isoptera, (d) Solifugae, (e) Hymenoptera, (f) Lepidoptera, (g) Hemiptera, (h) Passeriformes, and (i) small mammals (Rodentia and Soricomorpha) during each sample period throughout the nonbreeding season at Middelburg and Newcastle. Note different y-axis scales.

= 0.159; Fig. 2c, Table 3). Isoptera percentages peaked earlier at Newcastle than at Middelburg, with peaks occurring during JAN_{D3} and MAR_{D1} at Middelburg and during JAN_{D2} at Newcastle (Fig. 2c); these peaks were significantly different from the other sampling periods for each site (TukeyHSD: $P < 0.05$).

Overall, the percentage of Solifugae in the diets of the Newcastle falcons was higher than those from

Middelburg ($t = 6.589$, $df = 779$, $P < 0.001$; Fig. 1, Appendix 2). Solifugae percentages at Middelburg remained consistently low, with no significant differences through the season ($F = 1.313$, $df = 10$, $P = 0.222$). At Newcastle, Solifugae percentages differed significantly ($F = 3.138$, $df = 10$, $P < 0.001$; Table 3), decreasing from the beginning of the season until JAN_{D2}, (TukeyHSD: $P < 0.05$; Fig. 2d),

Table 3. Changes in the percentages of the main orders recorded in Amur Falcon (*Falco amurensis*) pellets throughout the nonbreeding season in Middelburg and Newcastle, using ANOVA test. Significant difference between sample periods indicated by *.

ORDER	MIDDELBURG			NEWCASTLE		
	df	F	P	df	F	P
Coleoptera	10	10.950	< 0.001*	10	2.228	0.015*
Orthoptera	10	10.710	< 0.001*	10	7.529	< 0.001*
Isoptera	10	14.640	< 0.001*	10	1.443	0.159
Solifugae	10	1.313	0.222	10	3.138	< 0.001*
Hymenoptera	10	5.320	< 0.001*	10	1.460	0.251
Lepidoptera	10	30.610	< 0.001*	10	30.610	< 0.001*

before levelling and then rising again significantly during MAR_{D2}.

Falcons at Middelburg had significantly higher overall percentages of Hymenoptera in their diet than did those at Newcastle ($t = 3.559$, $df = 779$, $P < 0.001$; Fig. 1, Appendix 2). The percentage of Hymenoptera in the diet differed throughout the season at Middelburg ($F = 5.320$, $df = 10$, $P < 0.001$), with a significantly higher percentage of Hymenoptera in MAR_{D3} (TukeyHSD; $P < 0.05$), but not at Newcastle ($F = 1.460$, $df = 10$, $P = 0.251$; Fig. 2e, Table 3). The percentage of Hymenoptera in the diet at each site peaked at different times, which was probably a consequence of different swarming events by the alates at each site. The Hymenoptera peaks also coincided with the peaks of Isoptera (Fig. 2c, e), with peaks occurring during JAN_{D3} and MAR_{D1} at Middelburg and JAN_{D2} at Newcastle (Fig. 2c, e).

Lepidoptera percentages at Middelburg were significantly higher than at Newcastle ($t = 4.181$, $df = 779$, $P < 0.001$; Appendix 2). As a result of a single peak during JAN_{D1}, the percentage of Lepidoptera in the diet differed significantly throughout the season at Middelburg ($F = 30.610$, $df = 10$, $P < 0.001$; Table 3). Percentages also differed significantly throughout the nonbreeding season at Newcastle ($F = 30.610$, $df = 10$, $P < 0.001$; Table 3). Lepidoptera percentages peaked at Middelburg during JAN_{D1}, then declined rapidly until there was no longer evidence of them in the diet at the end of the nonbreeding season, while at Newcastle percentages peaked significantly during DEC_{D2} (TukeyHSD: $P < 0.05$; Fig. 2f).

Overall Hemiptera percentages did not differ between sites ($t = 0.592$, $df = 779$, $P = 0.553$; Fig. 1, Appendix 2). Apparent peaks in the percentage of Hemiptera in the diet at both sites could not be investigated statistically due to the small sample size (Fig. 2g).

Vertebrate prey were categorized into two groups: birds (Passeriformes) and small mammals (Rodentia and Soricomorpha). The percentages of vertebrate prey in the diets of both the Middelburg and Newcastle falcons were smaller than the percentages of invertebrate prey; thus, the peaks observed throughout the season do not necessarily represent increased abundance at different periods in the season, but rather the increased proportions of remains observed in pellets. Passeriformes occurred less consistently but in higher percentages in the diet of the Middelburg falcons compared to falcons

from Newcastle (Fig. 2h), although the difference was not significant ($t = 1.908$, $df = 779$, $P = 0.057$; Appendix 2). Small mammals followed a similar trend to the Passeriformes, although significantly higher percentages of small mammals, mainly in the form of Rodentia, made up the diet of the Middelburg falcons ($t = 2.092$, $df = 779$, $P = 0.036$; Fig. 2i, Appendix 2).

Diet comparison among taxa. We examined the correlative relationships in dietary percentages of the five most abundant prey taxa to understand the patterns and the dietary variation through the nonbreeding season. The percentages of Coleoptera and Orthoptera were negatively correlated at both Middelburg ($r = -0.520$, $P < 0.001$) and Newcastle ($r = -0.612$, $P < 0.001$). During JAN_{D2}, the proportions of Coleoptera in the diet peaked while Orthoptera percentages decreased at both Middelburg ($F = 10.950$, $df = 10$, $P < 0.001$) and Newcastle ($F = 2.228$, $df = 10$, $P = 0.015$; TukeyHSD: $P < 0.05$; Fig. 2a, b). The increased percentages of Isoptera and Hymenoptera during JAN_{D2}, JAN_{D3}, and MAR_{D1} at Newcastle and Middelburg coincided with the declines in Coleoptera and Orthoptera (Fig. 2a, b, c, e). At Middelburg, Isoptera percentages were negatively correlated with both Coleoptera ($r = -0.325$, $P < 0.001$) and Orthoptera ($r = -0.373$, $P < 0.001$) and at Newcastle Isoptera were negatively correlated with Orthoptera ($r = -0.307$, $P < 0.001$). At Newcastle, the percentages of Isoptera and Lepidoptera were weakly correlated ($r = 0.095$, $P = 0.048$). The peaks in Isoptera and Hymenoptera occurred during the same sampling periods at both Middelburg and Newcastle (Fig. 2c, e). Solifugae were negatively correlated with the increased percentages of Isoptera at Middelburg ($r = -0.123$, $P = 0.018$; Fig. 2c, d). There was, however, no correlation between Isoptera and Solifugae at Newcastle although the peak in Isoptera during JAN_{D2} coincided with the decline in Solifugae percentages during the same sampling period (Fig. 2d).

The Jaccard cluster analysis revealed that there was no significant difference in the taxa consumed at either site, although there were sampling periods throughout the season which were similar, both within and between study sites (Fig. 3). The mean similarity between Newcastle and Middelburg was $65.9 \pm 15.1\%$. Newcastle showed significantly more within-site similarity ($75.6 \pm 13.3\%$) than Middelburg ($65.9 \pm 13.4\%$; t -test: $t = 3.810$, $P < 0.001$). Only DEC_{D3} and JAN_{D3} at Middelburg were similar,

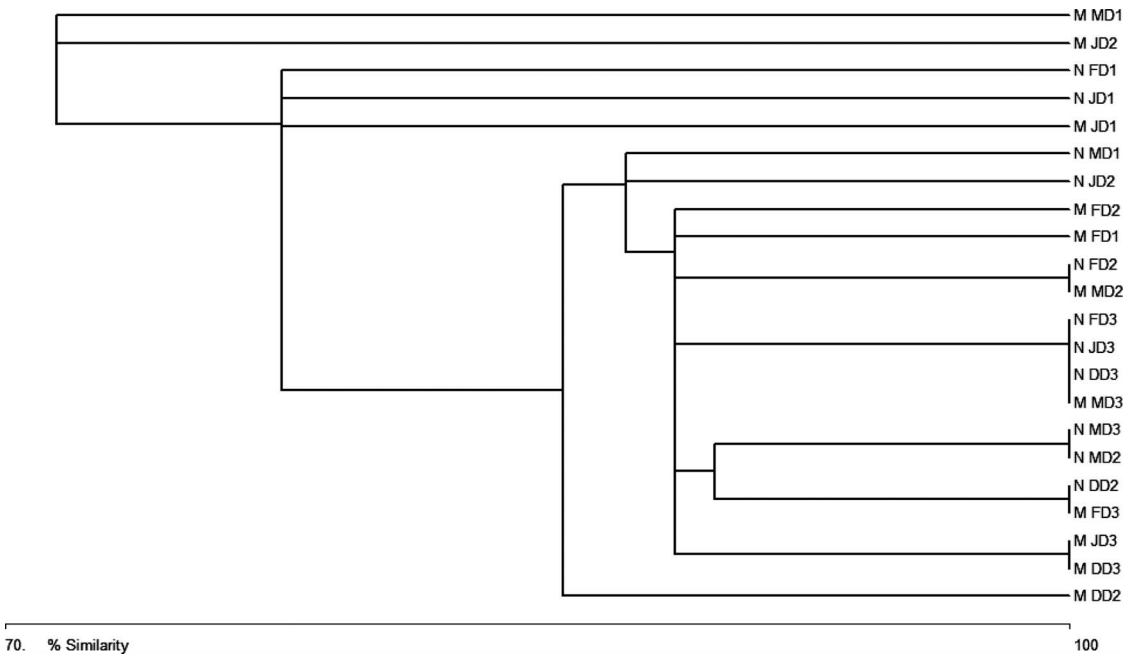


Figure 3. Similarity in diet (Jaccard cluster analysis) of Amur Falcons (*Falco amurensis*) during respective sampling periods at Middelburg (M) and Newcastle (N).

whereas DEC_{D3}, JAN_{D3}, and FEB_{D3}; and MAR_{D2} and MAR_{D3}, were similar at Newcastle (Fig. 3). Of the 121 possible comparisons of Middelburg to Newcastle, only five pair comparisons were identical, i.e., 100% similarity (Fig. 3).

DISCUSSION

Diet. Like Lesser Kestrels (McCann 1994, Kopij 1998, Anderson et al. 1999, Kok et al. 2000, Kopij 2002, 2005, 2007) and Amur Falcons from Lesotho and Bloemfontein (Kopij 2009, Pietersen and Symes 2010), Amur Falcons in the South African grasslands feed almost entirely on invertebrate prey while overwintering, but occasionally include vertebrate prey. All taxa observed in the Amur Falcon pellets collected from Middelburg and Newcastle have been documented in previous studies on other kestrel and falcon species in South Africa (Kemp and Filmer 1988, McCann 1994, Van Zyl 1994, Kopij 1998, Anderson et al. 1999, Kok et al. 2000, Kopij 2002, Ristow 2004, Kopij 2005, 2007, 2009, Pietersen and Symes 2010, Bouwman et al. 2012), except Soricomorpha, which is believed to be a new record. Falcons and other small raptors can be opportunistic when feeding on both invertebrates and vertebrates (Collopy and Koplín 1983, Kok et al. 2000,

Kopij 2007, Geng et al. 2009, Kopij 2009). Coleoptera, Orthoptera, Hymenoptera, Isoptera, and Solifugae remains have been recovered from the pellets of American Kestrel (*Falco sparverius*; Collopy and Koplín 1983), Eurasian Kestrel (*F. tinnunculus*; Fairley 1973, Franco and Andrada 1977, Fattorini et al. 2001, Souttou et al. 2006), Greater Kestrel (*F. rupicoloides*; Kemp and Filmer 1988), Lesser Kestrel (McCann 1994, Kopij 1998, Kok et al. 2000), and Eleonora’s Falcon (*F. eleonora*; Ristow 2004). This emphasizes the opportunistic feeding behavior of these raptors and the importance of the region as an abundant invertebrate prey source (Masman et al. 1986).

A large proportion of the grassland biome in South Africa is threatened by human modification, with approximately 30% irreversibly transformed (NGBP 2007) and only 1.6% formally protected (Neke and du Plessis 2004). At a national scale, any modifications in the grassland biome could potentially have implications on Amur Falcon populations as well as other migratory birds, particularly if prey abundance and availability are reduced (Dijkstra et al. 1988, Biber 1990, Donázár et al. 1993, McCann 1994, Mendelsohn 1997, Tella et al. 1998, Anderson et al. 1999, Buij et al. 2013). Grasslands

and open savannas are the stronghold for Lesser Kestrel and Amur Falcon populations in South Africa and it is critical for the persistence of these birds that these biomes be protected (McCann 1994, Jenkins 2005). However, the fact that some of the largest Amur Falcon roost sites are in areas greatly affected by land transformation suggests that the species is more resilient than might be anticipated. Nevertheless, because the threshold of modification at which Amur Falcons might no longer persist is currently unknown, we encourage a proactive approach to conserving this ecologically important species.

Land Transformation. The majority of the transformation observed at both sites is attributable to livestock farming, crop farming (especially maize), and afforestation (Mucina and Rutherford 2006), all of which employ pesticides. Prey abundance declines with increased land transformation and pesticide usage, and this in turn may affect foraging Amur Falcons through a reduction in prey availability (Cramp and Simmons 1980, Biber 1990, Donázar et al. 1993, McCann 1994, Keith and Bruggers 1998, Anderson et al. 1999). Middelburg has experienced greater land transformation than Newcastle (Mucina and Rutherford 2006) and we expected that prey percentages would be significantly different between the two sites; however, this was not the case. Amur Falcons consumed a greater percentage of vertebrate prey at Middelburg, which may be related to the increase in cultivated land, which might attract more rodents or make the rodents that are present more available to falcons.

Although the overall percentage of invertebrates consumed between the two sites did not differ, individual orders differed between Middelburg and Newcastle. Orthoptera and Solifugae percentages were significantly higher at Newcastle than at Middelburg, and this might have resulted from the increased vegetation cover in the form of crops and plantations in Middelburg (Blaum et al. 2009). The decline in certain taxa as a result of land transformation does reduce prey availability for Amur Falcons, but the increase in crops, livestock, and vegetation cover may attract alternate prey (Blaum et al. 2009). Therefore, land transformation may not be entirely detrimental to Amur Falcons, as these birds are opportunistic (Collopy and Koplin 1983, Kok et al. 2000, Kopij 2007, Geng et al. 2009, Kopij 2009) and have the ability to forage over vast areas of the subregion, tracking prey seasonally and

spatially during the overwintering period (Symes and Woodborne 2010).

The availability of taxa such as Solifugae, thought to be an important component of the diet (Anderson et al. 1999, Kopij 2005), may be significantly reduced with land transformation. However, Kopij (2009) found that Solifugae were not significantly affected by physical land transformations in Lesotho, as arthropod prey was abundant in both natural grasslands and cultivated land. In our study, reductions in the amount of Solifugae in the diet at Middelburg may be driven by various factors such as land transformation and pesticide use, which either directly or indirectly reduces the abundance of this taxon.

Importance of the Grassland Biome to Amur Falcon Diets. The warm, subtropical climate and seasonal rainfall of South Africa creates a region abundant in invertebrate prey, especially during the warmer summer period (November–February) when most rainfall occurs (Denlinger 1980, Masman et al. 1986). The abundance of prey offers easily accessible food for migratory birds, which they use to restore body condition after a lengthy migration (Masman et al. 1986, Dijkstra et al. 1988, Village 1990, McCann 1994, Anderson et al. 1999). Lesser Kestrels pause their molt prior to migration and continue molting once they reach their overwintering grounds (McCann 1994); this behaviour may also be used by Amur Falcons, as these birds migrate a greater distance than Lesser Kestrels over the same period (Jenkins 2005, Symes and Woodborne 2010). Molt requires increased nutrients and the abundant invertebrate prey in South Africa likely supplies these resources (Masman et al. 1986, Dijkstra et al. 1988, Village 1990, McCann 1994).

It is evident in prey percentages that certain taxa, i.e., Isoptera, Hymenoptera, and Lepidoptera, are consumed in greater percentages at certain periods during the nonbreeding season, which likely results from invertebrate swarming events (Bouwman et al. 2012). Migratory falcons may time their arrival in the breeding or nonbreeding grounds with these irruptions (Moreau 1952, Dijkstra et al. 1988, Buij et al. 2013). Isoptera, in particular, are heavily exploited by Amur Falcons and other kestrel species across South Africa (Moreau 1952, Cramp and Simmons 1980, Kemp and Filmer 1988, McCann 1994, Anderson et al. 1999, Kopij 2007, Bouwman et al. 2012). The observed peaks of Isoptera in prey remains at Middelburg and Newcastle suggest that

these swarming events are important in the diet and that Isoptera may be preferred to other species. These swarming events do not appear to coincide with the arrival of Amur Falcons as previously suggested (Moreau 1952), but do offer an abundant prey source throughout the nonbreeding season. However, the resolution at which we sampled may have been too coarse to detect irruptions that occur at smaller time scales, and this needs to be further investigated.

While overwintering in South Africa, Amur Falcons feed on a variety of invertebrates, some of which are agricultural pest species. These taxa include Coleoptera (e.g., *Heteronychus arator*; Pietersen and Symes 2010) and Orthoptera and Isoptera (e.g., *Odontotermes badius*; Picker et al. 2001). The presence of these species in the diet of Amur Falcons suggests that the birds may be important contributors to pest control (Pietersen and Symes 2010, Bouwman et al. 2012).

Seasonal Variation of Diet. The Amur Falcon's diet changes throughout the season, as does the Lesser Kestrel's (Kopij 1998, Anderson et al. 1999, Kok et al. 2000, Kopij 2002, 2005, 2007). Generally Amur Falcons fed on Coleoptera at the beginning of the nonbreeding season, but as the season progressed Coleoptera percentages decreased and Orthoptera increased in the diet, possibly as a result of seasonal rainfall changes (Kopij 2007). The observed changes in the percentage of prey taxa in the diet may be a response to changes in actual abundance of the respective taxa or may reflect the tracking of prey by Amur Falcons when it becomes available.

Lesser Kestrels consumed more prey toward the end of the nonbreeding season (McCann 1994) and their body fat conditions also increased, possibly due to increased Orthoptera intake (Anderson et al. 1999), which becomes more important prior to migration. Isoptera and Hymenoptera were generally eaten when the alates were irrupting after rainfall events (Leuthold and Bruinsma 1977, Korb and Salewski 2000). Certain rainfall events may be more important to invertebrate swarming events, as the swarming events occur sporadically, and Isoptera and Hymenoptera peak during the same or similar sampling periods during the nonbreeding season. Climatic changes could result in changes in rainfall patterns, which in turn may lead to decreased or unpredictable alate swarming. This could in turn affect the prey available to Amur Falcons.

The patterns of Coleoptera and Isoptera in the diet of Amur Falcons differ from that previously reported for Lesser Kestrel diets (McCann 1994, Kok et al. 2000). However, this may simply be a result of spatial differences between study sites or an atypical, wetter period during the current study (Kopij 2005). The small proportion of sampling periods that were similar within and between study sites, and the reduced similarity in percentages among sampling periods at Middelburg, suggest that there is dietary change or at least variability within the region during the season. Solifugae was one of the five most abundant taxa observed in both the Middelburg and Newcastle diets and was consistent proportionally throughout the season, suggesting that Solifugae are important to the diet of Amur Falcons and could buffer the diet during periods of shift from Coleoptera to Orthoptera. Higher Solifugae percentages were recorded during a drier season by Kopij (2005). Therefore, the differences between Newcastle and Middelburg, and the fact that the study occurred in a wetter season than usual, suggest that Solifugae may not be influenced as much by precipitation as previously thought, but rather more so by land transformation (Blaum et al. 2009). Additional taxa that may potentially be part of the diet of Amur Falcons but were not detected in the pellets, such as soft-bodied prey (e.g., Lepidoptera and Diptera), would result in reductions of the apparent importance of the aforementioned taxa (Kopij 2009).

The Amur Falcon is a versatile species capable of feeding on a wide range of invertebrate and occasionally vertebrate prey. They are also capable of shifting their diet throughout the season and likely respond to invertebrate population irruptions, both spatially and temporally. It is suggested that they move between different roost sites during the nonbreeding season, and in so doing track abundant prey where and when it is available (Symes and Woodborne 2010). This behavior may explain why they are able to persist in anthropogenically transformed areas and why they have become so successful within the South African grasslands. Not only are these falcons capable of surviving anthropogenic changes, but they offer an important ecological service.

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Appendix 1. Taxa identified from Amur Falcon (*Falco amurensis*) regurgitated pellets collected at Middelburg and Newcastle between 11 December 2012 and 31 March 2013, showing the number of prey items/order.

ORDER	NUMBER PER ORDER		FAMILY	SUB-FAMILY	GENUS
	MIDDELBURG	NEWCASTLE			
Coleoptera	3705	4020	Carabidae Curculionidae Elateridae Scarabaeidae	Cetoniinae Scarabaeinae	
Orthoptera	2724	4469	Acrididae Gryllidae		
Isoptera	2481	2316	Termitidae	Macrotermitinae	<i>Odontotermes</i>
Solifugae	236	1328			
Hymenoptera	583	278	Formicidae	Formicinae	<i>Camponotus</i>
Lepidoptera	230	38			
Hemiptera	22	25	Reduviidae Scutelleridae		
Passeriformes	50	23			
Rodentia	48	3	Muridae		
Soricomorpha	6	6	Soricidae		
Total	10,103	12,506			

Appendix 2. Differences in the dietary percentages of prey orders consumed by Amur Falcons (*Falco amurensis*) at Middelburg and Newcastle. Significant differences between sites are marked with an * (*t*-test: $P < 0.05$).

ORDER	<i>t</i>	<i>P</i>
Coleoptera	1.398	0.162
Orthoptera	3.871	< 0.001*
Isoptera	4.006	< 0.001*
Solifugae	6.589	< 0.001*
Hymenoptera	3.559	< 0.003*
Lepidoptera	4.181	< 0.001*
Hemiptera	0.592	0.554
Passeriformes	1.908	0.057
Rodentia	2.092	0.037*
Soricomorpha	0.005	0.996