

Migratory connectivity and conservation of the Amur Falcon *Falco amurensis*: a stable isotope perspective

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Summary

Stable isotopes (δD , $\delta^{13}C$, $\delta^{15}N$) were measured in adult and juvenile Amur Falcon *Falco amurensis* feathers to understand the migratory connectivity of this species. Using the OIPC (Online Isotopes in Precipitation Calculator) and a calibration curve for American Kestrels *Falco sparverius* we predicted the breeding range of South African Amur Falcons in the Palaearctic. δD values for juvenile feathers (mean \pm SE = $-58.1 \pm 2.5\text{‰}$, range -83.9 to -25.7‰) and predicted Palaearctic annual precipitation values indicated that juvenile Amur Falcons in South Africa originated from across their entire Palaearctic range. This rejects the leapfrog migration hypothesis and suggests the widespread movement of birds south, with a funnelling effect into the subregion where they become concentrated over a narrower distribution range. Adult δD_f values were more depleted ($-37.4 \pm 1.8\text{‰}$, range = -71.3 to -9.3‰) than predicted annual precipitation values for sites where feathers moulted in South Africa ($-20.2 \pm 0.9\text{‰}$) but there was no correlation between δD_p and δD_f . This, together with significant variation of $\delta^{13}C$ among sites and annual fluctuations in roost sizes, suggests that roost site fidelity is low in the overwintering range. Populations not confined to breeding sites in South Africa are able to move widely across the subregion, feeding on a broad range of arthropods that become seasonally abundant during the austral summer. Total population estimates for South Africa are significantly lower than global estimates so a significant proportion of the population may not overwinter in South Africa or global populations are significantly lower than estimated. In South Africa, roosts that number hundreds to thousands of individuals are often in large exotic trees, e.g. *Eucalyptus* sp. They are often tolerant of disturbance at roosts which may be of little concern for their conservation. Habitat changes in the overwintering range in South Africa though, particularly due to agriculture, afforestation and strip mining, may affect global population numbers. There is also concern over the persecution of birds along their migratory route.

Introduction

The migration of raptors constitutes one of the most spectacular movements of predators on earth (Bildstein and Zalles 2005). Because of their trophic status, raptors act as useful flagship species for conservation (Bildstein *et al.* 2000). The greatest threat to migratory raptors is habitat loss, so understanding their migration patterns is important for effective conservation strategies (Alerstam 1990, Bildstein *et al.* 2000). Little is known about the migratory movements of many raptor species, particularly those moving between Asia and Africa (McClure 1998) despite recent advances in satellite telemetry that have contributed to understanding movements of some species (Meyburg *et al.* 1995, Kjellen *et al.* 1997, Meyburg *et al.* 2001, Trierweiler *et al.* 2007). The application of the technique is limited by the lower limit of transmitter size, currently ~ 5 g (Strandberg *et al.* 2009) which prevents similar studies on smaller migrants. The lightest

species tracked to date has recently decreased from the Eurasian Hobby *Falco subbuteo* Linnaeus 1758 (mass = c. 230 g; Strandberg *et al.* 2009) to the Red-footed Falcon *F. vespertinus* Linnaeus 1766 (mass = c. 135 g).

It is important in the conservation and long-term survival of migratory raptors, particularly in the context of global climatic changes and rapid habitat modification due to human activity, to determine their migratory origins. *En route* migratory stopover points may be critical for many species (Bildstein *et al.* 2000), but equally important are the final “over-wintering” destinations where the build-up of resources for the coming breeding season may be crucial (Sanderson *et al.* 2006). In the southern African subregion there is a funnelling effect of migrants from an extensive longitudinal range in the northern hemisphere (Newton 1995, Bildstein and Zalles 2005, Dingle 2008). This has implications for the conservation of many migrant species that “over-winter” in South Africa during the austral summer because the population is concentrated over a smaller area in their non-breeding African range.

Of particular concern is the Amur Falcon *Falco amurensis* Radde 1863, a small (male, 137.6 g, $n = 18$, female, 159.5 g, $n = 26$; Schäfer 2003) insectivorous raptor that undergoes a one-way migration of ~13,000 km (Ferguson-Lees and Christie 2001, Mendelsohn 1997, Jenkins 2005). This includes the longest regular over-water passage of any raptor, flying over the Indian Ocean between south-western India and East Africa, a distance of c. 4,000 km (Cade 1982, Ali and Ripley 1987, Orta 1994, Mendelsohn 1997, Bildstein *et al.* 2000, Birdlife International 2008). It breeds over a wide range in Mongolia, Siberia and northern China, although little has been documented on its distribution in the Palaearctic (Cheng 1987, Mendelsohn 1997, Ferguson-Lees and Christie 2001, Bildstein and Zalles 2005, Global Raptor Information Network 2008). Birds arrive in southern Africa during November to early December and roost in colonies that number thousands of individuals (Benson 1951, Cade 1982, Tarboton and Allan 1984). For a number of months they are a common sight on the eastern Highveld, before departing north again during April to May (Mendelsohn 1997, Jenkins 2005).

Stable hydrogen isotopes have been used to determine migratory connectivity of numerous species in the Americas and Europe (e.g. Chamberlain *et al.* 1997, Hobson 2008, Chamberlain *et al.* 2000, Meehan *et al.* 2001, Hobson *et al.* 2004a,b). On a global scale, the distribution of δD_p is relatively predictable, with a general depletion (more negative δ values) in δD_p with an increase in latitude (Bowen and Revenaugh 2003). The assimilation of this water during feather growth, at different latitudes, can then be used to indicate the origins of birds (Hobson and Wassenaar 2008). On a broad scale, the relationship between the isotope signature of precipitation (δD_p) and that of feathers (δD_f) is usually linear, with δD_f values being 20–50‰ depleted (more negative) than that of δD_p values (Meehan *et al.* 2001, Wassenaar and Hobson 2001, Wassenaar and Hobson 2003, Hobson and Wassenaar 2008). This understanding of δD patterns has been particularly useful in determining the movement patterns and migratory origins of long distance migrants across the globe (e.g. Hobson and Wassenaar 1997, Hobson and Wassenaar 2008). Within Africa the hydrogen isotope gradient on either side of the equator is low, so movements of birds within the continent are more difficult to study using stable isotopes (but see Yohannes *et al.* 2005, Yohannes *et al.* 2007, Wakelin *et al.* in press).

Distinct isotope fractionation processes occur during the C_3 and C_4 photosynthetic pathways, resulting in unique isotope signatures for each vegetation type that animals feed on; C_3 plants are typically more depleted in ^{13}C relative to C_4 and CAM plants (Park and Epstein 1960, Park and Epstein 1961, Smith and Epstein 1971, Vogel *et al.* 1978, Ehleringer 1991, Dawson *et al.* 2002). Also, the distributions of C_3 and C_4 plants are associated with broad-scale global patterns of plant distribution (Stowe and Teeri 1978). Studies of animal tissues that reflect diet can therefore be good indicators for interpreting the use of different resources (C_3 or C_4) on temporal and spatial scales (e.g. Cerling *et al.* 2006). On the other hand, nitrogen isotopes are a useful tool in understanding trophic ecology because each step in a food chain is usually associated with an isotopic enrichment of 3–5‰ from diet to animal tissue (Peterson and Fry 1987, Mizutani *et al.* 1992, Kelly 2000, Post 2002). Nitrogen and carbon are therefore useful

elements in identifying carbon sources and delineating trophic levels of organisms (Minagawa and Wada 1984, Peterson and Fry 1987, Hobson and Wassenaar 1999).

Accordingly, stable isotope data from feathers of South African Amur Falcons were analysed to address specific questions concerning migratory connectivity and local movements in the overwintering range of this species. Because Amur Falcons breed in the northern hemisphere we expected stable hydrogen isotopes in the feathers of juveniles to reflect their origins. Adults, on the other hand, undergo a complete flight feather moult in southern Africa (Northern Flagship Institution unpubl. data), so isotopes in feathers were expected to reflect the area in which the feathers grew. Some feathers (i.e. P4–6 and S5–7) appear to moult in the Palaearctic (Schäfer 2003) and are not re-moulted in southern Africa. To complement analyses using hydrogen isotopes, we used stable carbon and nitrogen isotopes that provide further information on diet, to provide additional support for answering questions relating to movements of Amur Falcons. More specifically, we attempted to answer the following questions; 1) Can we determine the breeding origins of birds in the Palaearctic? 2) Do Amur Falcons display a leap-frog migration pattern, i.e. northernmost breeding birds overwinter furthest south? 3) Do members of roosting flocks originate from similar regions in the northern hemisphere? 4) Do populations exhibit roost fidelity in the South African subregion?

Materials and Methods

Feather collection

Specimens of individual adult male and female and juvenile male and female Amur Falcons that were killed during a thunderstorm on 25 December 2004 at a roost in Ventersdorp were collected for analysis (Bernitz 2006). These specimens, housed in the Transvaal Museum, Pretoria, were surgically sexed and used as a feather identification reference for additional samples collected from beneath roosts throughout South Africa during December 2008–March 2009. The museum specimens were also sampled. Details of sites and number of samples collected at each site are given in Table 1.

Sample preparation and isotopes analysis

Feathers were washed in distilled water to remove faecal matter, followed by cleansing in a 2:1 chloroform:methanol solution to remove surface oils and contaminants (Hobson *et al.* 2003, 2004a). $^{13}\text{C}/^{12}\text{C}$ isotope ratios are given relative to Vienna Pee Dee Belemnite (VPDB), $^{15}\text{N}/^{14}\text{N}$ ratios relative to Air and $^2\text{H}/^1\text{H}$ ratios relative to Vienna Standard Mean Ocean water (VSMOW), with values expressed in δ notation in parts per thousand (per mille, ‰).

Table 1. Amur Falcon feather collection sites in South Africa (ordered from northernmost to southernmost) and number of samples collected at each site.

Location	Grid reference	Altitude m a.s.l.	Adult female	Adult male	Juvenile	TOTAL
Naboomspruit	24°25'01'S 28°55'01'E	1,098	5	5	4	14
Middelburg	25°46'30'S 29°27'57'E	1,490	5	5	7	17
Ventersdorp	26°19'36'S 26°49'18'E	1,349	5	5	10*	20
Heidelberg	26°30'15'S 28°21'26'E	1,482	8	5	1	14
Newcastle	27°46'14'S 29°56'27'E	1,185	5	5	11	21
Graaff-Reinet	32°15'41'S 24°32'14'E	719	0	0	3	3
Pearston	32°34'59'S 25°08'12'E	704	1	0	0	1
			29	25	36	90

*Five male and five female specimens. Details of Transvaal Museum specimens are given in Appendix 1.

For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses, representative samples (0.15–0.30 mg) were weighed in tin cups (pre-cleaned in toluene) and combusted at 1,020°C in an Elemental Analyser (Flash EA, 1112 Series, Thermo Electron Corporation, Bremen, Germany). The $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ isotope ratios were then determined using a Thermo Delta V Plus continuous-flow isotope ratio mass spectrometer (CFIRMS) (Thermo Electron Corporation) plumbed in-line with the elemental analyser via a ConFlo IV gas controller (Thermo Fisher Scientific, Bremen, Germany). Two aliquots of a laboratory standard (homogenised dried chicken blood; mean $\delta^{13}\text{C} \pm \text{SD} = -17.87 \pm 0.15\text{‰}$, $n = 331$) were used for every six to eight unknowns in sequence. In order to correct for equipment drift, duplicates were run for each sample. The laboratory standard was standardised against C652 ANU sucrose, 1577b bovine liver (National Institute of Standards and Technology) and SRM 1547 peach leaves (NIST).

In order to discount the exchangeable hydrogen fractionation we used a comparative equilibration approach where samples are equilibrated with the same ambient water vapour as working standards with known non-exchangeable δD values (Wassenaar and Hobson 2003). Feather samples (0.15–0.30 mg) and keratin working standards (BWB-II = $108 \pm 4\text{‰}$, CFS = $138 \pm 5\text{‰}$, CHS = $187 \pm 2\text{‰}$; Wassenaar and Hobson 2003) were weighed into silver cups and stored for 72 hr at room temperature prior to analysis. The $^2\text{H}/^1\text{H}$ ratios were measured using a high temperature TC/EA elemental analyzer (Thermo Fisher Scientific, Bremen, Germany) with pyrolysis at 1,450 °C that was coupled to the CFIRMS. A linear regression model fitted between measured *vs* actual δD values for the three keratin working standards was used to correct the δD values of the feather samples (Wassenaar and Hobson 2003).

Data analyses

All mean values are presented \pm SE, unless otherwise stated. Where data were normally distributed we conducted t-tests and where data were not normally distributed we conducted a non-parametric Mann-Whitney U-test, between adult and juveniles, and males and females. For comparisons between sites we used an ANOVA where data were normally distributed and a Kruskal-Wallis test where data were not normally distributed. Comparisons of δD in adult feathers with the predicted δD values of precipitation for the site where the feathers were collected (in South Africa) were made using a simple bivariate regression model. We calculated the δD (‰ VSMOW) value of precipitation for each site where feathers were collected in South Africa using The Online Isotopes in Precipitation Calculator (OIPC) (Bowen *et al.* 2005, Bowen 2009). To predict the origins of juveniles we calculated the δD values for precipitation (where the birds originated) by using a calibration curve derived for American Kestrels *Falco sparverius* (Hobson *et al.* 2009). This calibration curve was derived from known-source *F. sparverius* feathers (from Lott and Smith 2006), and predicted growing-season δD in precipitation (from Bowen *et al.* 2005). We cannot be sure of the proportion of prior precipitation that contributes to tail feather growth of juveniles. This is because a broad range of integration from the environment, representing a wider temporal period than simply the integration of D during the month of feather growth, is likely. We therefore used an annual mean δD value of precipitation throughout the breeding range to predict the D in precipitation that contributed to feather growth (Hobson *et al.* 2009). In the northern Palaearctic the mean growing season average of precipitation δD values, as an estimate of mean hydrogen isotope input to the food webs, is typically used and is usually defined as those months where temperature is $> 0^\circ\text{C}$. In temperate regions this may also include snow. However, until there is a good δD feather map for the Palaearctic this interpretation will remain an issue. Tail feathers of juveniles grow mostly during June (Schäfer 2002). We therefore expected the diet of Amur Falcons in their breeding range, which includes a wide range of invertebrate and small vertebrate prey (e.g. birds, rodents, amphibians; Schäfer 2003); to represent precipitation many months prior to feather growth. The predicted δD values of precipitation that indicated the origins of juvenile feathers were then overlaid with the distribution range of Amur Falcons in the Palaearctic to indicate the likely

origins of juveniles that we sampled in South Africa (Ferguson-Lees and Christie 2001, S. Gombobaatar unpubl. data). We also overlaid this distribution with precipitation δD values (that indicated the origins of juvenile feathers) for the month (June) when juvenile feathers grew, but do not present the data.

Results

Shapiro-Wilk's test for normality indicated that data were normally distributed for δD ($W = 0.9859$, $P = 0.46$) but not normally distributed for $\delta^{15}N$ ($W = 0.9673$, $P = 0.02$) and $\delta^{13}C$ ($W = 0.9267$, $P < 0.01$).

The δD values for juveniles were significantly depleted compared to adults (adults = $-37.4 \pm 1.8\text{‰}$, range = -71.3 to -9.3‰ ; juveniles = $-58.1 \pm 2.5\text{‰}$, range = -83.9 to -25.7‰ , $t = -6.87$, $df = 86$, $P < 0.001$; Figure 1). There was no significant difference among sites for juveniles (ANOVA, $F_{5,29} = 0.984$, $P = 0.44$) or adults (ANOVA, $F_{4,48} = 0.930$, $P = 0.45$). The δD values for adult males and females were similar (male = $-37.2 \pm 2.5\text{‰}$, female = $-37.6 \pm 2.6\text{‰}$, $t = 0.087$, $df = 51$, $P = 0.93$). Also, δD values did not differ among sites for males (ANOVA, $F_{4,20} = 0.280$, $P = 0.887$) or females (ANOVA, $F_{4,23} = 1.174$, $P = 0.348$) (Figure 1).

Values for $\delta^{13}C$ between adults and juveniles were not significantly different, (Mann-Whitney $U = 807.0$, $P = 0.174$, adults $-18.6 \pm 0.4\text{‰}$, juveniles = $-19.3 \pm 0.5\text{‰}$). For adults there was a significant difference among sites (Kruskal-Wallis test: $H_{5,54} = 15.33$, $P = 0.009$) with a post-hoc test determining Ventersdorp adults ($\delta^{13}C = -15.5 \pm 0.7\text{‰}$) to be more enriched than Newcastle adults ($\delta^{13}C = -19.6 \pm 1.1\text{‰}$) ($P = 0.03$). For juveniles, although there was no significant difference among sites (Kruskal-Wallis test: $H_{4,34} = 7.63$, $P = 0.11$), although post-hoc tests revealed Ventersdorp ($-17.9 \pm 0.8\text{‰}$) to be more enriched than Graaff-Reinet ($-21.8 \pm 0.4\text{‰}$), Middelburg ($-20.0 \pm 0.9\text{‰}$) and Naboomspruit ($-17.5 \pm 2.8\text{‰}$), and Newcastle ($-20.3 \pm 0.7\text{‰}$) more enriched than Graaff-Reinet ($P < 0.05$) (Figure 1).

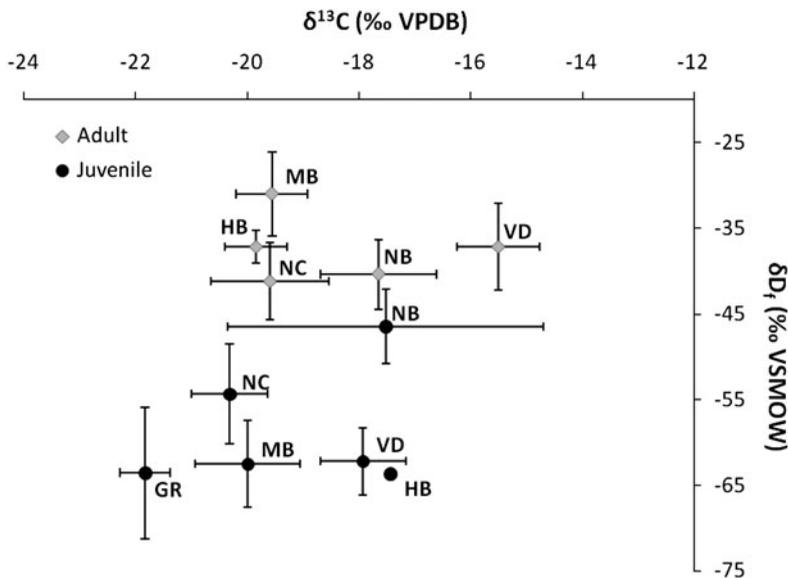


Figure 1. Mean $\delta^{13}C$ (VPDB) and δD (VSMOW) (‰ \pm SE) values of feathers for adult and juvenile Amur Falcons from different roost sites in South Africa. See Table 1 for details of sites and sample sizes. MB = Middelburg, GR = Graaff-Reinet, NB = Naboomspruit, NC = Newcastle, HB = Heidelberg, VD = Ventersdorp.

Values for $\delta^{15}\text{N}$ were similar between adults and juveniles (Mann-Whitney $U = 911.0$, $P = 0.61$, adults = $7.6 \pm 0.3\text{‰}$, juveniles = $7.3 \pm 0.4\text{‰}$). For adults and juveniles there was no difference among sites (Kruskal-Wallis test: $H_{5,54} = 4.33$, $P = 0.50$ and $H_{5,36} = 5.33$, $P = 0.38$, respectively; Table 2).

Using a global model of δD in precipitation we calculated predicted annual values of δD ($-20.2 \pm 0.9\text{‰}$, $n = 5$ sites), for each site in South Africa where we collected adult feathers (Bowen *et al.* 2005, Bowen 2009). Adult δD_f values ranged from -71.3‰ to -9.3‰ (mean = $-37.4 \pm 1.8\text{‰}$) and mean site values were all more depleted ($3.0 - 18.4\text{‰}$) than predicted annual precipitation (δD_p) values. The δD_f values of adult feathers from the respective roost sites was not correlated with δD_p values at each site (Bowen *et al.* 2005, Bowen 2009) (D_f adults = $-64.108 - 1.3213 * \text{D}_p$, $F_{1,3} = 2.51$, $P = 0.21$) (Table 2).

Predicting δD_p values for sites where juveniles fledged was more difficult because we did not know their origins. Also, the Palaearctic distribution of Amur Falcons is poorly documented, with breeding recorded as far south as Bhutan (see Figure 2; Baker 1935 in Feijen and Feijen 2008). The mean value for juvenile feathers (δD_f) was -58.8‰ which was well within expected values throughout the range of Amur Falcons in the Palaearctic (Figure 2; OIPC, Bowen 2009). Juvenile δD_f values ranged from -83.9 to -25.7‰ . We predicted δD_p values within the range of Palaearctic Amur Falcons to range from -80.1‰ to -46.1‰ (Figure 2; Table 3; Hobson *et al.* 2009). We therefore overlaid the range of δD_p values from -85‰ to -40‰ to indicate the regions, within their known range, from where juvenile Amur Falcons originated (Figure 2; Table 3).

Discussion

The Eastern Palaearctic to South Africa

Because juvenile flight feathers of birds sampled in South Africa were grown on the nest in the Palaearctic, they were expected to represent the breeding origin of birds (Hobson and Wassenaar 1997, Meehan *et al.* 2001, Wassenaar and Hobson 2001, Hobson *et al.* 2004b). Most stable isotope studies on raptor species show a depletion in δD of feathers from precipitation of $37-52\text{‰}$ (Lott *et al.* 2003, Meehan *et al.* 2003). To predict the region where feathers of juveniles were grown we used a calibration curve determined for American Kestrels *Falco sparverius* that accounted for fractionation of D from local annual precipitation to feathers (Hobson *et al.* 2009). We recorded a wide range (-83.9 to -25.7‰) of feather δD values of juveniles with all predicted values for juveniles falling well within the range of expected annual δD_p values of their Palaearctic distribution range. Not surprisingly, the northern limit of where juveniles were predicted to have originated (i.e. predicted northern limit of breeding range for birds sampled in

Table 2. Mean ($\text{‰} \pm \text{SE}$, AIR) $\delta^{15}\text{N}$ values of adult and juvenile feathers for different roost sites in South Africa, mean predicted δD values ($\text{‰} \pm \text{SE}$, VSMOW) for precipitation during the moult period (December-February) of Amur Falcons at different feather collection sites and mean δD values ($\text{‰} \pm \text{SE}$, VSMOW) of feathers collected at respective sites during December 2008 – March 2009. Sample size in parentheses.

Site	$\delta^{15}\text{N}$		δD	
	Adult	Juvenile	Precipitation	Adult
Naboomspruit	7.8 ± 0.8 (10)	7.2 ± 0.4 (4)	-22.0 ± 1.2	-40.4 ± 4.0 (10)
Middelburg	6.9 ± 0.7 (10)	6.2 ± 0.9 (7)	-28.0 ± 1.2	-31.0 ± 4.9 (10)
Ventersdorp	8.3 ± 0.5 (10)	8.2 ± 0.7 (10)	-25.0 ± 1.2	-37.2 ± 5.1 (10)
Heidelberg	7.2 ± 0.8 (13)	6.1 (1)	-27.0 ± 1.2	-37.2 ± 1.9 (13)
Newcastle	7.4 ± 0.9 (10)	7.5 ± 0.8 (11)	-25.3 ± 1.2	-41.2 ± 4.5 (10)
Graaff-Reinet	–	6.6 ± 1.1 (3)	-21.7 ± 0.7	–
Pearston	9.7 (1)	–	-22.3 ± 0.3	–
Mean	7.6 ± 0.3 (54)	7.3 ± 0.4 (36)	-25.0 ± 2.7	-37.4 ± 1.8 (53)

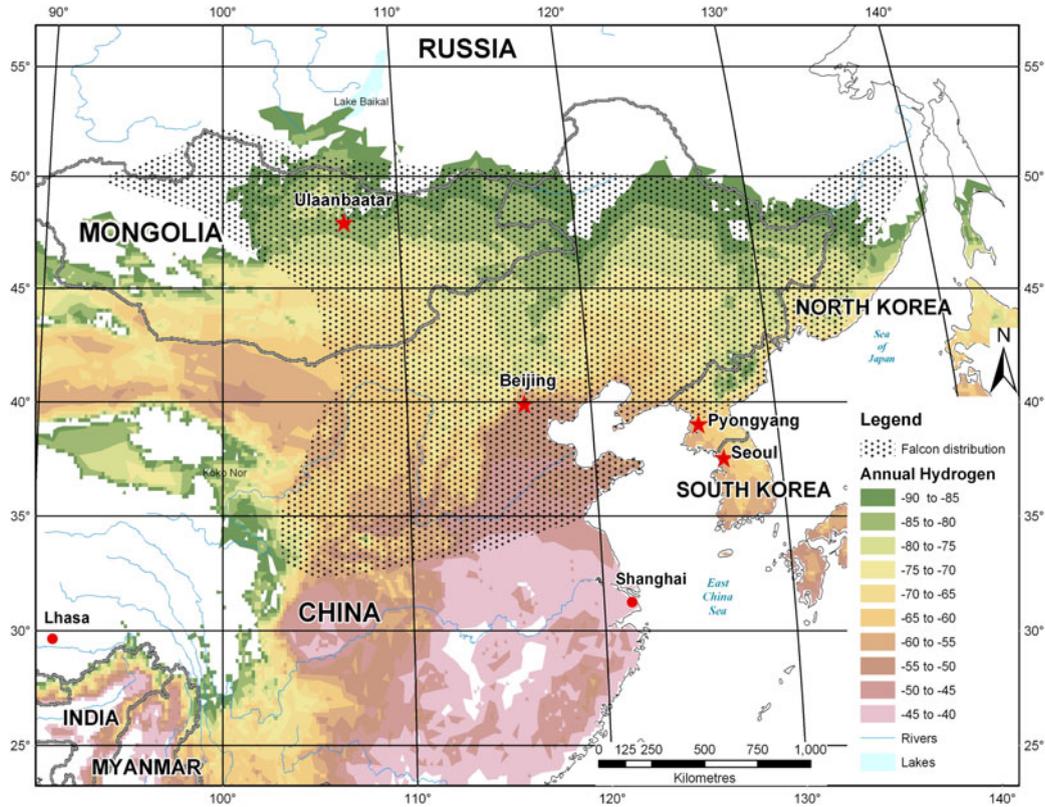


Figure 2. Distribution of Amur Falcon *Falco amurensis* in the eastern Palearctic during the boreal summer (modified from Moreau 1972, Ferguson-Lees and Christie 2001, S. Gombobaatar unpubl. data), and regions within the range (δD) of precipitation, Bowen *et al.* 2005, Bowen 2009) that correspond to likely δD_F values of juvenile Amur Falcons sampled in South Africa (Hobson *et al.* 2009; see Table 3). The isotopic range of δD_{pr} from where the birds are likely to have originated was determined using a calibration curve for American Kestrels *Falco sparverius* (Hobson *et al.* 2009). Missing δD plots on the map do not fit within this range of predicted values, and become more depleted with an increase in latitude north.

Table 3. Minimum, maximum and mean values (\pm SE) (‰ , VSMOW) for juvenile feathers collected in South Africa with predicted δD values (‰ , VSMOW) of precipitation in Northern Hemisphere where feathers are likely to have grown. Predicted precipitation values calculated using calibration curve for American Kestrels ($\delta D_f = 53.06 + 1.71 * \delta D_p$, $n = 41$; Hobson *et al.* 2009).

Site	Feather			Precipitation			n
	Min	Max	Mean	Min	Max	Mean	
Naboomspruit	-55.5	-35.2	-46.5	-51.6	-63.5	-58.2	4
Middelburg	-78.4	-44.5	-62.5	-57.1	-76.9	-67.6	6
Ventersdorp	-72.6	-32.8	-62.2	-50.2	-73.5	-67.4	10
Heidelberg	-	-	-63.7	-	-68.3	-68.3	1
Newcastle	-83.9	-25.7	-54.3	-46.1	-80.1	-62.8	11
Graaff-Reinet	-71.3	-48.2	-63.6	-59.2	-72.7	-68.2	3
Mean	-72.3	-58.1	-58.8	-46.1	-80.1	-65.0	35

South Africa) correlates well with the known northern limit of the distribution of Amur Falcons in the Palaearctic. Rather than attempting to pinpoint the origins of individual birds, we focused on assigning the origins of juveniles to a broad geographic band within the known range of breeding Amur Falcons (Langin *et al.* 2007). Our findings therefore suggest that juveniles in South Africa originated from throughout their distributional range in the Palaearctic (Figure 2, Wassenaar and Hobson 2001, Bowen and Revenaugh 2003, Hobson and Wassenaar 2008). However, birds from a region west of Ulaanbaatar, Mongolia, appear not to have been sampled. This may reflect an absence of birds from this region in South Africa or simply inconsistencies in our method of analysis. Amur Falcons have been recorded breeding north of Ulaanbaatar and 378 individuals have been ringed in a study there (Schäfer and Stubbe 2005). However, none of these individuals have been recovered in their "overwintering" grounds. This is more likely a reflection of the low numbers of recoveries and difficulties in catching birds in their overwintering range.

Because there is temporal variation in the δD values of precipitation we cannot be sure that hydrogen contributions to feather growth reflected values for an entire annual period, rather than δD values of precipitation for June, the month in which juveniles grew tail feathers (Schäfer 2005). However, we consider the former scenario more likely because prey of Amur Falcons will probably reflect the signature of prey that had assimilated resources representing a broader time period prior to feather growth. It is, however, interesting to note that when precipitation values in the breeding range are considered for June, the origins of juveniles sampled in South Africa extends further north than their known distribution in the Palaearctic. Although plausible, this seems less likely.

On global and regional scales the distribution of C_3 and C_4 grasses has been well documented with C_4 grasses largely restricted to warmer climates and (lower latitudes and altitudes) (e.g. Teeri and Stowe 1976, Stowe and Teeri 1978, Vogel *et al.* 1978, Hattersley 1983). Also, there is a general decrease in the proportion of C_4 grasses with an increase in latitude (cooler climates). We therefore expected enriched (more positive) $\delta^{13}C$ values, representing carbon input from a C_3 dominated system, to reflect a more northerly origin for juveniles (Kelly *et al.* 2002). For juveniles sampled in South Africa there was a general trend of northern-most birds representing a stronger C_4 dietary signature, and more southerly populations having a stronger C_3 signature. In the northern hemisphere the diet of juveniles includes a greater proportion of mammals, birds and amphibians (Schäfer 2003, Pietersen and Symes 2010) so the link between $\delta^{13}C$ values and latitude is less plausible for inferring breeding origins of South African birds. A more adequate explanation is that the wide range of $\delta^{13}C$ values represents the variable ingestion of prey items from C_3 and C_4 sources.

Carbon input from the environment may therefore not be a good indicator of latitudinal origin because of diet switching between C_3 and C_4 resources at a site, or the broad spatial use of resources by adults feeding nestlings. This pattern is also reflected in the wide range of $\delta^{13}C$

values of adult feathers in South Africa suggesting that birds within a roost are not all relying on the same food source, or food type, and that they are sourcing their diet from both C_3 and C_4 systems. Carbon sourced from both C_3 and C_4 in different adult individuals from the same roost may thus reflect, i) a wide feeding niche with reliance on C_3 (strong broadleaved or high altitude and/or altitude grassland influence) to C_4 (low altitude and/or altitude grassland) and/or crops (e.g. maize), and/or, ii) the sampling of birds whose feathers had grown with resources beyond that reflected in the vicinity of the roost. This latter point is supported by the lack of a positive correlation between the δD_f values of adult feathers and the mean δD_p of precipitation at the sites where feathers were collected, i.e. sites where feathers were presumed to have moulted if adult Amur Falcons were faithful to roost sites.

Roosting in colonies

The 2009 National Kestrel Count Day (24 January) recorded 111,291 Amur Falcons at 32 roosts in South Africa (www.kestreling.com). This annual national count has, over the past five years recorded significant changes in roost sizes, with some roosts being abandoned (www.kestreling.com). Also, it represents only a fraction of the estimated global population of 100,000–1,000,000 birds (Global Raptor Information Network 2008, BirdLife International 2008). Usually roosts are active over several consecutive years, although numbers within each roost are known to vary within and between seasons (www.kestreling.com). These changes may reflect a movement of birds across the subregion and real changes in Amur Falcon numbers at regularly counted roost sites. In addition they may reflect an absence of birds in the subregion, adding support to the idea that a large proportion of birds do not reach South Africa to overwinter. The proportion of the population not reaching South Africa may overwinter further north and we suggest that it comprises birds starting their migration later (Figure 2). These birds probably overwinter in Namibia, Zambia, Zimbabwe, Malawi and Mozambique, with some birds remaining as far north as Tanzania (Mendelsohn 1997, Stevenson and Fanshawe 2002, Jenkins 2005). Other overwintering sites remain to be investigated and could likely include the Indian sub-continent (Mendelsohn 1997, Jenkins 2005).

The δD values of adult feathers, as predicted, were more depleted relative to predicted δD values in precipitation. Adults undergo a near complete moult in South Africa (Schäfer 2003) so we expected feathers to represent the site at which they were collected (see Hobson and Wassenaar 2008). There was no correlation of δD_f values with δD_p suggesting that feathers grown in South Africa did not grow at the roost site where they were collected (OIPC, Bowen 2009). It is unknown whether roost site fidelity is high within a season, or whether the same birds return to the same roost site each year. Given these data, and large variation in roost counts between years, we suggest that roost site fidelity is low, with a prolific movement of birds across the southern African subregion both within and between years. Because individual birds are not fixed to a specific site by breeding they are able to wander, feeding on the episodic and patchy occurrence of food resources such as crop pests (e.g. maize pests), and grasshopper and termite alate irruptions (Brown 1971, Brown *et al.* 1982, Pietersen and Symes 2010).

Most grasses within the range of Amur Falcon in South Africa are C_4 although the diet of falcons is not confined to arthropods reliant on this vegetation type (Vogel *et al.* 1978, Mendelsohn 1979, 1997, Jenkins 2005, Pietersen and Symes 2010). If all adult Amur Falcons at a roost site were feeding on a similar diet during the period of feather growth in South Africa we would expect them to have similar carbon isotope values in feathers. This was not the case and diet studies indicate they feed on wide range of invertebrates (Mendelsohn 1979, 1997, Jenkins 2005, Kopij *in press*, Pietersen and Symes 2010). The wide range of $\delta^{13}C$ values is therefore associated with a variable diet and foraging over a wide area to access these food sources.

Rectrices were used because they can be readily aged and sexed and are freely available below roosts as part of the normal moult process. However, they may not be the best feathers for isotope studies because they are much more likely to be dropped and replaced irregularly and not as part

of the normal physiological moult processes e.g. during escape from predation. The wide range of samples (and outliers) for adults and juveniles may therefore be the result of irregular moult patterns and not identification error. Remiges may have yielded better results but with the current sampling method, ageing and sexing of remiges would not have been possible.

Trophic position

In the open savanna environment where Amur Falcons were recorded, the $\delta^{15}\text{N}$ values of invertebrates found in the grass (C_4) and wooded vegetation (C_3) over five months were sampled and mean values (\pm SD) of $4.7 \pm 1.4\text{‰}$ and $6.3 \pm 1.9\text{‰}$ recorded respectively ($n = 15$ each) (Symes *et al.* unpubl. data). This suggests that the values for adults ($7.6 \pm 0.3\text{‰}$) are in line with a typical open savanna/grassland invertebrate diet, being an estimated one trophic position above the invertebrates in this system. Values of juveniles and adults were similar suggesting that in South Africa and the Palaeartic Amur Falcons feed at a similar trophic level in both regions. In South Africa the diet of Amur Falcons has been shown to include solifugids, beetles, termites but seldom rodents and birds (Mendelsohn 1997, Jenkins 2005, Kopij in press, Pietersen and Symes 2010). However, dietary information on juveniles suggests otherwise; mammals, birds and amphibians appear to be more important dietary items for nestlings (Schäfer 2003). *En route* diets are not known and difficult to interpret from stable isotope analysis and it is unknown whether Amur Falcons rely on stop-over feeding sites during migration. Their migration patterns may be timed to take advantage of prevailing weather conditions, moving ahead of the ITCZ with the shifting of seasons, much the same as dragonfly migrations between Africa and India (Anderson 2009). During the non-breeding period of Amur Falcons in South Africa, the irruption of termite alate and crop-pest species, important food sources, may often be unpredictable and patchy; in the Palaeartic this may be less so, although a wide range of $\delta^{15}\text{N}$ values suggests a nitrogen input from a range of trophic levels for both adults in South Africa and juveniles in the Palaeartic.

Conclusions

The status of the Amur Falcon is currently unclear and there is little evidence for recent changes in its distribution and numbers in Africa (Mendelsohn 1997, Global Raptor Information Network 2008, BirdLife International 2008). In light of recent findings that the total number of birds recorded in South Africa alone is significantly below that estimated for the total world population, either a significant proportion of the population overwinter north of South Africa or the global estimate is significantly over-inflated (Global Raptor Information Network 2008, BirdLife International 2008, A. van Zyl pers. comm.). The grassland regions within their South African range, upon which they are reliant for foraging, is under threat from agriculture, afforestation and open-cast mining (Mendelsohn 1997, Jenkins 2005). Stomach content analysis suggests that Amur falcons forage successfully over maize monoculture (Pietersen and Symes 2010) indicating some flexible adaptation to anthropogenic changes. Also, the isotopic evidence suggests that the niche occupied by the Amur Falcons during their stay in South Africa is cosmopolitan, with a broad dietary base and opportunistic exploitation of wide spatial ranges. Before the conservation status of the species can be concluded, the niche bottlenecks associated with migration and breeding at other locations on their annual migration also need to be considered. For example reports of large scale capture of migrating birds at important stopover sites in northern India are cause for concern (Tan 2009). In the northern hemisphere, the picture is less clear, and although the entire population may disperse over a breeding range far greater ($\sim 4,000,000 \text{ km}^2$) than the South African range ($\sim 500,000 \text{ km}^2$), similar factors may affect its conservation there. The species is categorised globally as a species of "Least Concern" by BirdLife International (2008). With rapid changes in human population growth and the associated impacts on the environment, more information is required to ensure the long term persistence of this long-distance migratory raptor.

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Appendix A. Specimen numbers of Amur Falcons from Ventersdorp sampled at the Transvaal Museum, Pretoria (Northern Flagship Institution).

No	Age	Sex	Code
1	Adult	Male	TM78635
2			TM78686
3			TM78704
4			TM78717
5			TM78728
6		Female	TM78718
7			TM78741
8			TM78854
9			TM78867
10			TM78869
11	Juvenile	Male	TM78639
12			TM78687
13			TM78699
14			TM78716
15			TM78871
16		Female	TM78684
17			TM78706
18			TM78709
19			TM78711
20			TM78723