Survival of Sooty Falcons (Falco concolor) *breeding in Oman*

M. J. McGrady, W. A. Al Fazari, M. H. Al Jahdhami, J. E. Hines & M. K. Oli

Journal of Ornithology

ISSN 2193-7192
Volume 157
Number 2

J Ornithol (2016) 157:427-437
DOI 10.1007/s10336-015-1302-6

Springer

J Ornithol (2016) 157:427–437
DOI 10.1007/s10336-015-1302-6

ORIGINAL ARTICLE

Survival of Sooty Falcons (*Falco concolor*) breeding in Oman

M. J. McGrady[1] · W. A. Al Fazari[2] · M. H. Al Jahdhami[2] · J. E. Hines[3] · M. K. Oli[4]

Received: 14 April 2015 / Revised: 15 September 2015 / Accepted: 12 October 2015 / Published online: 29 October 2015

Abstract Although the Middle East supports a high level of avian biodiversity, the ecology of relatively few species that use the region has been studied in detail. Despite its restricted breeding distribution in the Middle East, and apparent unfavorable conservation status, little is known about the population ecology of the Sooty Falcon (*Falco concolor*), one of only two falcon species that breeds in the boreal summer. We applied multi-state models to capture–mark–recapture data collected during 2007–2014 in the Sultanate of Oman to estimate, for the first time, the probabilities of capture, age-specific breeding probabilities, and state-specific apparent survival for Sooty Falcon. Capture probability for breeding adults (±1SE) was 0.443 ± 0.088. Annual apparent survival probability for pre-breeders and for breeding adults was 0.570 ± 0.048 and 0.656 ± 0.069, respectively. The probability that 2-, 3-, and 4-year-old falcons returned as breeders was 0.065 ± 0.036, 0.159 ± 0.069, and 0.339 ± 0.211, respectively. In 2013, we radio-tagged five fledgling falcons, and monitored their fates using satellite-based tracking. All initiated their first migration and survived for 48 days following radio-tagging, but four of the five birds died by 70 days post-tagging; only one survived >100 days. Our results suggest that only about 12 % of fledglings survive to the average age of first breeding (~3.8 years), and that most of first-year mortality occurs during their first migration or soon after they reach their destination. Low apparent survival of pre-breeders could result in low recruitment to the breeding population, and population declines. A comprehensive population-level assessment is urgently needed to accurately determine the status of Sooty Falcons, and to devise flyway-scale conservation plans.

Keywords State-specific survival · Age-specific breeding probability · Capture–mark–recapture analysis · *Falco concolor* · Sooty Falcon demography · Multi-state models · Sultanate of Oman

Zusammenfassung

Überlebenschance von brütenden Schieferfalken (*Faclo concolor*) im Oman

Obwohl es im Nahen Osten ein hohes Maß an Artenvielfalt gibt, wurden in dieser Region nur relativ wenige Arten untersucht. So wissen wir trotz der eingeschränkten Brutverteilung im Nahen Osten und dem ungünstigen Schutzstatus wenig über die Populationsökologie des Schieferfalken (*Falco concolor*), eine von zwei Falkenarten, die dort im borealen Sommer brüten. Wir sammelten Fang-/Wiederfang-Daten im Sultanat von Oman von 2007–2014. Wir verwendeten *multi-state models*, um Fangwahrscheinlichkeit, altersspezifische Brutwahrscheinlichkeit und Überlebenschance des Schieferfalken zu schätzen. Die Fangwahrscheinlichkeit für brütende adulte

Communicated by C. Barbraud.

✉ M. J. McGrady
mikejmcgrady@aol.com

[1] International Avian Research, Am Rosenhügel 59, 3500 Krems, Austria

[2] Office for Conservation of the Environment Diwan of Royal Court, P.O. Box 246, 100 Muscat, Sultanate of Oman

[3] United States Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708, USA

[4] Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, USA

Schieferfalken betrug 0,443 ± 0,088 (±1 SE). Die jährliche Überlebenswahrscheinlichkeit für immature Vögel war 0,570 ± 0,048, die für adulte Brutvögel 0,656 ± 0,069. Die Wahrscheinlichkeiten, dass 2-, 3-, und 4-jährige Falken als Brutvögel zurückkommen, betrugen 0,065 ± 0,036, 0,159 ± 0,069 bzw. 0,339 ± 0,211. 2013 haben wir fünf junge Falken mit Satellitensendern ausgestattet. Alle begannen ihren ersten Zug und überlebten die ersten 48 Tage nach der Besenderung. Vier von fünf Vögeln starben jedoch innerhalb von 70 Tagen nach der Besenderung. Nur einer überlebte für mehr als 100 Tage. Unsere Ergebnisse zeigen, dass nur etwa 12 % der Jungvögel bis zum Durchschnittsalter von Erstbrütern (~3.8 Jahre) überleben und dass die höchste Sterberate im ersten Jahr während der ersten Migration auftritt oder kurz, nachdem die Vögel ihr Ziel erreicht haben. Die niedrige Überlebensrate von immaturen Vögeln könnte zu einem geringen Recruitment in die Brutpopulation führen und somit zu einem Rückgang der Population. Eine umfassende Studie des Schieferfalken ist dringend notwendig, um seinen genauen Schutzstatus zu bestimmen und Schutzmaßnahmen für die Zeit der Wanderung zu entwickeln.

Introduction

The Middle East, which includes the countries of southwest Asia and North Africa extending from the Libya–Egypt border in the west to Afghanistan in the east, Turkey in the north and Yemen in the south, is important to a great variety of bird species. Despite popular perception, the biodiversity of the region is in fact higher than some northern temperate areas (Evans 1994). The breeding ranges of about 440 bird species overlap with the region, more than 60 species are endemic, and millions of birds migrate through the area along the Africa–Eurasian flyway (Porter and Aspinall 2010). Many avian species of conservation concern, including some that are Critically Endangered (e.g., Slender-billed Curlew *Numeneus tenuirostris*, Sociable Lapwing *Vanallus gregarious*), occur in the region. National laws and flyway-scale initiatives like Bird Life International's Migratory Soaring Bird's Project (http://www.migratorysoaringbirds.undp.birdlife.org/) and the Convention on Migratory Species'(CMS) "Raptor's MOU" (http://www.cms.int/raptors/en/page/agreement-text) highlight the concern for raptors using the region. Despite this interest, demographic data are lacking and the ecology of most avian species using this region is poorly understood. Estimates of survival, reproduction and population growth rates, and the factors influencing these rates, are essential for conservation planning (Oli et al. in press), but this information is not available for most avian species breeding or wintering in the Middle East.

The Sooty Falcon (*Falco concolor*) is a small to medium-sized falcon with a restricted breeding range in the Middle East and north-eastern Africa. It spends the non-breeding season (winter) mostly in Madagascar, while Egypt, Eritrea, Saudi Arabia and Oman are the main breeding strongholds (Walter 1979a, b; Del Hoyo et al. 1994; Gaucher et al. 1995; Semere et al. 2008). Most published information on this species is from its breeding grounds in Oman (Walter 1979a, b), Israel (Frumkin and Pinshow 1983; Frumkin 1988, 1993), Saudi Arabia (Gaucher et al. 1988, 1995) and Bahrain (Kavanagh and King 2008). The Sooty Falcon is closely related, and ecologically similar, to the Eleonora's falcon (*F. eleonorae*), which is better studied (e.g., Walter 1979b; Ristow et al. 1991; Gschweng et al. 2008; López-López et al. 2010). Both species breed in the boreal summer, sometimes in aggregations on islands, feed their offspring primarily on small passerine birds migrating between the Palearctic and their African wintering areas, and spend the non-breeding season in Madagascar, where insects are an important part of their diet. Into the 1990s, guestimates of Sooty Falcon population size were of 40,000 breeding pairs or 100,000 individuals (Walter 1979a, b; Del Hoyo et al. 1994; Ferguson-Lees and Christie 2001). More recently, Gaucher et al. (1995) noted that there were probably only about 500 breeding pairs in Arabia, and, based on this, surmised the global population to be <1000 breeding pairs. Kavanagh and King (2008) re-examined the existing data and concluded that the global estimate of 1000 breeding pairs was reasonable. Consequently, the Sooty Falcon's conservation status was downgraded to Near Threatened. Birdlife International (2015) puts the global population at 10,000–19,999 individuals), but this guestimate is not based on empirical data. The small breeding populations in the United Arab Emirates (UAE) and Bahrain (Kavanagh and King 2008; Shah et al. 2008) and the larger population in Oman (McGrady and Nicoll 2008) are thought to be declining. However, estimates of demographic parameters or population growth rates and causes of population declines remain unknown. As such, population ecology of Sooty Falcons is poorly understood, and there exist no published reports of survival or reproductive parameters for this species.

The ecologies of the falcon species that share the most typical annual cycle (i.e. spring breeding) are fairly well studied (e.g., Ratcliffe 1980; Village 1990; Hiraldo et al. 1996). While many aspects of the ecology of Sooty and Eleonora's Falcons are probably similar to those of falcons that nest in the boreal spring, it is not unreasonable to believe that there are important differences, including, for example, characteristics of the prey base. Understanding these differences may provide ecological insight that can help conserve other predatory birds, especially as prey abundance, distribution, and availability change.

We studied population ecology of Sooty Falcons breeding on the Daymaniyat Islands and Fahal Island, Sultanate of Oman, during 2007–2014. Using multistate capture–mark–recapture (CMR) modeling approaches and 7 years of field data, we provide the very first estimates of state-specific annual apparent survival and age-specific breeding probabilities for Sooty Falcons anywhere in its range. Finally, we used Kaplan–Meier methodology (Williams et al. 2001; Pollock et al. 1989) to analyze survival of satellite radio-tagged juvenile falcons to gain detailed insights regarding the timing and location (natal or wintering grounds, or migration route) of juvenile mortality.

Methods

Study area

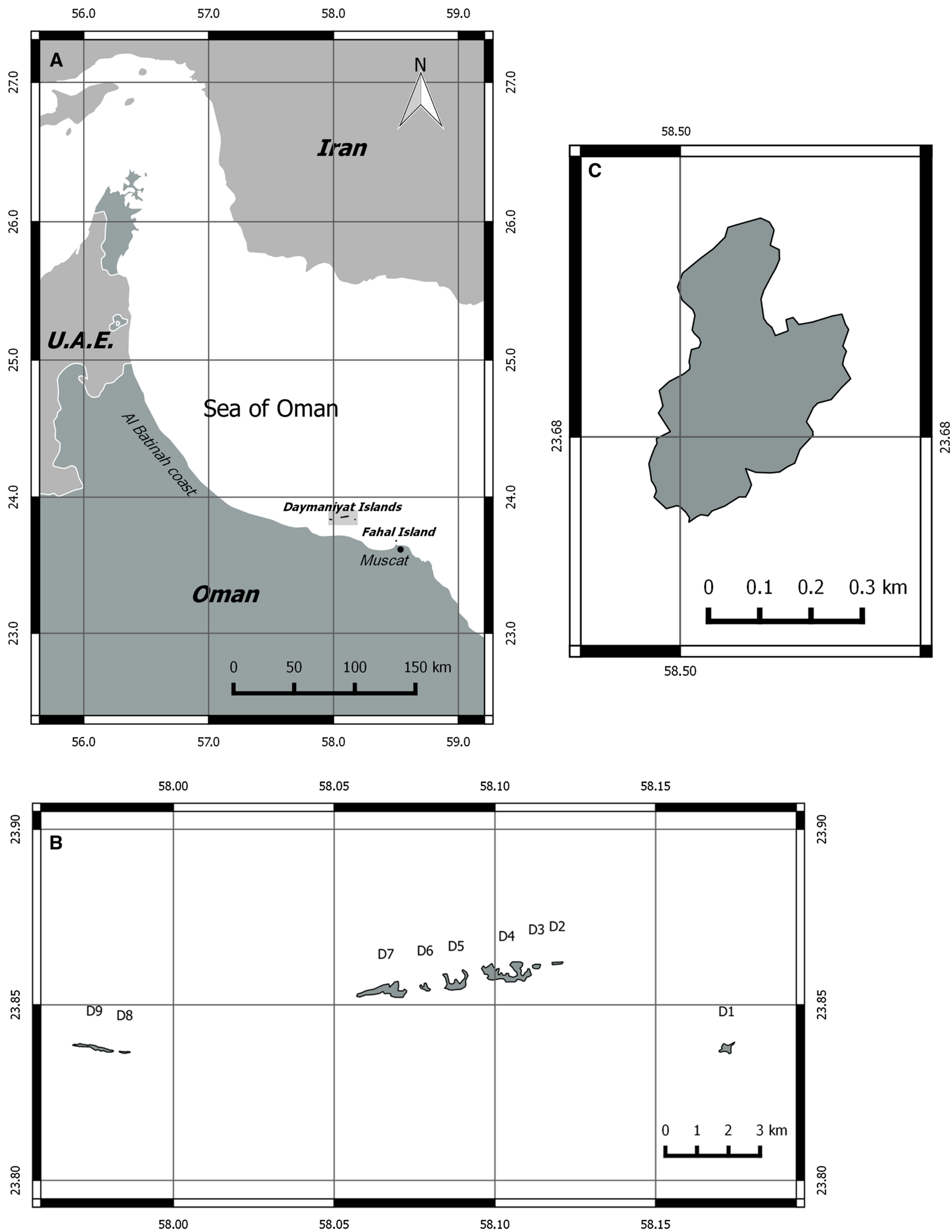
The study area comprised Fahal and the Daymaniyat Islands, Sultanate of Oman (Fig. 1). Fahal Island is an Eocene-aged (55–35 million years old) limestone, marl and coral crag island that covers 0.127 km^2 and lies about 3.5 km offshore from Muscat, the capital city of the sultanate. There are high (10–40 m), sometimes overhanging, cliffs on almost all sides and the island features steep valleys radiating out from its more or less central summit. Fahal Island is covered by loose gravel and boulders, and supports very little vegetation. Across the island, including in the cliffs, are numerous holes, crevices, and overhung ledges that provide good nesting locations (shaded and with a sandy floor) for Sooty Falcons (Walter 1979a, b), many of which are difficult or impossible to access. Fahal Island is an Important Bird and Biodiversity Area (IBA) because of the nesting Sooty Falcons (Evans 1994). Access to Fahal is controlled by the Royal Oman Police, and landing is difficult, especially at low tide or when the sea is not calm. Despite it being in a popular area for fishing, diving and snorkeling, few visitors land on the island, and the breeding falcons are generally undisturbed.

The Daymaniyat Islands are located about 55 km west-northwest of Muscat (about 37–56 km west of Fahal Island), and lie about 15 km offshore. They comprise nine islands arranged fairly linearly east to west over about 21 km. They are composed mostly of limestone, marl and coral crag with some shallow soils and areas of beach. They range from low sandy islands covered in some areas with relatively dense vegetation, dominated by *Sueda aegyptiaca*, to barren islands with precipitous cliffs that face mostly north. These cliffs and rocky areas provide numerous shaded places above the splash line of the sea where Sooty Falcons nest (Walter 1979a, b). The largest of the Daymaniyats is Jebel al Kabir (D4, 0.46 km^2); the smallest is Little Jun (D8, 0.01 km^2). In this paper, the islands are identified as D1 (easternmost, Jazirat Kharaba) to D9 (westernmost, Jazirat Jun). The Daymaniyat Islands and surrounding waters are a National Nature Reserve and an Important Bird Area due to breeding seabird colonies and the Sooty Falcons (Evans 1994). The islands are under the jurisdiction and management of the Ministry of Environment and Climate Affairs. Diving, snorkeling and landing are controlled by permits. There is a ranger outpost located on D4 (Al Jebel al Kabir). Other than the occasional overnight stay by rangers and researchers, the islands are uninhabited, but fishermen, divers and casual tourists land on some islands fairly regularly, staying mostly for periods of a few hours.

Field methods

We visited all the islands during two bouts of field work each year: egg stage (August) and late nestling stage (September–October). During the egg stage, we aimed to locate as many nests as possible and visit those that could be accessed. We sought to record occupancy of territories (defined here as areas containing nests and defended by breeding falcons), a task that was easy on smaller islands or islands with fewer suitable nesting locations, but was difficult on Fahal Island, where >50 % of nests were inaccessible and some occupied territories were indiscernible because no good view could be had, either from the sea or from the land. From 2008, we captured and sometimes recaptured breeding falcons at accessible nests using nooses and dummy eggs (Gosler 2004), and recaptured previously marked birds using PIT (Passive Induced Transponders) rings and a microchip reading device (Smith and McGrady 2009).

Our main aim during the egg stage was to capture as many breeding birds as possible given the available time, human resources, boats and equipment, determine the occupancy of territories and record clutch sizes. Because of the heat (sometimes reaching 50 °C), we typically worked from about 0630–1130 hours, then 1530–1830 hours. We searched each island for territorial pairs and nests. When we found the first nest, we would record its location, the age of the territory holders (by plumage: juvenile, subadult, and adult) and the number of eggs, place a PIT tag reader in the nest and search for the next nest. After all our readers were deployed, we would set a trap at the next nest, and try to trap a falcon. PIT tag readers were usually at nests for 1–2 h before they were retrieved; subsequent physical trapping occurred at nests where previously unmarked birds bred. Not all trapping was successful, and we abandoned trapping efforts at some sites due to time constraints.


A
N
Iran
U.A.E.
Sea of Oman
Al Batinah coast
Daymaniyat Islands
Fahal Island
Muscat
Oman
0 50 100 150 km
56.0
57.0
58.0
59.0
27.0
26.0
25.0
24.0
23.0
C
0 0.1 0.2 0.3 km
58.50
23.68
B
D1
D2
D3
D4
D5
D6
D7
D8
D9
0 1 2 3 km
58.00
58.05
58.10
58.15
23.90
23.85
23.80

◀**Fig. 1** The study area (QGIS desktop 2.6 http://www.qgis.org/en/site/), Sultanate of Oman. **a** Regional map; **b** Daymaniyat Islands; **c** Fahal Island

Additionally, some nesting sites were inaccessible, so our trapping efforts targeted only accessible nests with eggs.

Morphometric measurements were taken of breeders that were captured during the egg stage, and a blood sample was taken for genetic analysis. Unringed birds were fitted with an alphanumeric ring (British Trust for Ornithology, BTO), and a PIT tag in a plastic snap-on ring (similar to that described in http://unikon-system.com/en/products/pigeon-rings/). During the nestling period, we returned to the nests we had discovered during the egg stage, and searched for nests we might have missed. During this part of the field work, we recorded brood sizes, obtained morphometric measurements from nestlings, and collected a blood sample for genetic analysis. Nestlings were also fitted with both BTO and PIT rings. We also placed the PIT tag reader in newly found nests in case either of the breeders was fitted with a PIT ring.

Effort varied across years, and the timing of field work was not always ideal; in some years, nestlings started fledging before we arrived. In 2007 and 2011, no effort was made to capture falcons during the August field season, although we were able to identify two breeders from PIT rings in 2011 during the nestling-stage field work. With time, we became more efficient at finding nests and identifying breeders, so that in later years we covered the islands just as well as in former years, but in less time. The main impediment to ringing birds was the inaccessibility of some nests.

Capture–mark–recapture (CMR) analyses

We applied multistate CMR models to field data collected during 2007–2014 to estimate state-specific apparent survival and capture probability, and age-specific breeding probability (i.e. probability of pre-breeders becoming breeders for the first time (Williams et al. 2001; Spendelow et al. 2002; Lebreton et al. 2003). We considered two states: pre-breeders (fledging until they returned to the study sites as breeding adults) and breeders. We set capture probability (p) for pre-breeders to zero because, once ringed and released, birds ringed as nestlings were never again encountered as pre-breeders. Sooty Falcons did not breed during their first year, and the vast majority of known-aged birds had started breeding by age 5 years (see "Results"). Consequently, we set breeding probability of juveniles (i.e. first-year birds) to zero and that of birds age 5 or older to be one, and estimated probability of breeding for 2-, 3-, and 4-year-old birds, using an approach described by Lebreton et al. (2003). Finally, we estimated state-specific annual apparent survival probability (ϕ). Data limitations did not permit construction and analysis of meaningful alternative models, so we focused on estimating the aforementioned parameters. CMR analyses were performed in program MARK (White and Burnham 1999) v.6.2 implemented using the RMark package for program R (Laake and Rextad 2015) v.2.15.2.

Satellite radio-tracking and Kaplan–Meier survival analysis

In 2013, five juvenile Sooty Falcons from Fahal Island were fitted with backpack satellite-received radio transmitters (Platform Transmitter Terminal; PTTs) just prior to fledging (29 September–5 October), using a Teflon© ribbon (Bally Ribbon Mills, Bally, PA, USA) harness (Kenward 2001). Transmitters weighed 9.5 g, and were solar-powered PTT-100 models manufactured by Microwave Telemetry (Columbia, MD, USA) which had a transmission cycle of 10 h on and 48 h off. For all birds, PTTs were 3–4 % of falcon body mass at the time of fitting tags. PTTs also had sensors for activity, temperature, and battery charge. Information gathered using these sensors and location data were used in some instances to determine the likely fate of radio-tagged individuals. We used Kaplan–Meier methodology (Pollock et al. 1989; Williams et al. 2001) for estimating the survival curve for radio-tagged birds.

Results

Of the 476 falcons ringed, 37 were first ringed as breeders. Thirty-two falcons (7.77 %) were recaptured: 23 were recaptured once, and 9 were recaptured ≥ 2 times. Birds that were physically captured returned to the nest soon after capture. There was no evidence that trapping had a negative effect on productivity: 100 % of nests where at least one breeder was caught went on to produce at least one nestling. Also, breeders whose nests contained PIT tag reading equipment showed little or no reluctance to return to the nest.

Some 439 nestlings were fitted with rings during the study (Table 1); of these, 17 (3.9 %) were recaptured as breeders. Mean age of known-aged falcons ($n = 17$) at first breeding was 3.76 ± 1.48 (median = 3, range 2–6) years. Four 2-year-old breeders were captured, and the oldest known-aged breeder was a 7-year-old female. Of birds that were tagged as juveniles and subsequently returned as breeders, eight were reared on Fahal Island and nine on the Daymaniyats. Seven of eight nestlings (87.5 %) reared on Fahal came back to breed there, and one bred on the Daymaniyats. Six out of nine nestlings (66.7 %) raised on the Daymaniyats came back to breed on those islands,

Table 1 Number of Sooty Falcons (*Falco concolor*) ringed each year (2007–2014) in the Sultanate of Oman

Year	Number of nests accessed/estimated number of occupied territories[a]	Number of unringed breeders caught	Number of ringed breeders caught	Number of nestlings ringed
2007	39/81	0	0	62
2008	34/74	15	0	81
2009	44/56	9	3	37
2010	31/71	3	10	58
2011	28/66	0	1	56
2012	23/58	3	10	48
2013	26/62	4	13	63
2014	19/54	3	9	34

[a] Fahal Island was difficult to survey for occupied territories because of its topography, and accounts for most of the imprecision of the estimates of numbers of occupied territories. Estimates of number of occupied sites on Fahal varied between 32 in 2009 and 44 in 2010

Table 2 Summary of tracking via satellite of juvenile Sooty Falcons reared in Oman

ID	Sex	Date transmitter fitted	Migration departure date	Date of last moving signal	Days monitored	Days alive after migration	Location of last moving transmission
EX11690	Unknown	29/09/2013	08/11/2013	04/12/2013	66	26	Adigrat, Ethiopia
EX11676	Female	29/09/2013	07/11/2013	17/11/2013	49	10	Red Sea near Eritrea
EX11678	Female	30/09/2013	31/10/2013	03/08/2014	307	276	Yibal, Oman
EX11679	Male	05/10/2013	30/10/2013	14/12/2013	70	45	Mariakani, Kenya
EX11667	Male	29/09/2013	04/11/2013	14/11/2013	46	10	Bishah, Saudi Arabia

while three moved to Fahal to breed. Two of the six nestlings that showed nesting fidelity to the Daymaniyats as breeders, bred on the same island on which they were raised, while four bred on different islands in the chain.

None of the 12 breeders caught on Fahal and recaptured in subsequent years moved to any of the Daymaniyat Islands. None of the 19 breeders caught on any of the Daymaniyat Islands and recaptured in subsequent years moved to Fahal. Two falcons breeding on a Daymaniyat island moved 2.52 and 0.78 km to other islands in the chain in a subsequent year.

Capture probability ($\pm$1SE) for breeding adults was 0.443 ± 0.088. Annual apparent survival probability for pre-breeders and breeders was 0.570 ± 0.048 and 0.656 ± 0.070, respectively. Thus, the probability of fledglings surviving to the average age of first breeding (3.76 years) was: $0.570^{3.76} = 12.08\,\%$. Finally, age-specific annual breeding probability for 2-, 3-, and 4-year-old falcons was 0.065 ± 0.036, 0.159 ± 0.069, and 0.339 ± 0.211, respectively.

Of the five juvenile falcons fitted with radio transmitters, none survived 1 year. The earliest mortality of a radio-tagged bird was recorded 49 days after tagging, and 10 days after migration had commenced. However, mortality increased rapidly thereafter; four birds died by the 70th day and one survived 307 days (Table 2). The probability of survival to 68 days was 0.333 ± 0.192, and median survival time was 55 days. Mortality occurred in Saudi Arabia, Eritrea, Ethiopia, Kenya and Oman. The bird that survived 307 days died in Oman, but far from any breeding locations, the nearest being about 180 km away in UAE.

Discussion

Population dynamics and persistence are inherently governed by population growth rates, which in turn are functions of demographic parameters such as survival and fecundity rates (Caswel 2001; Oli and Armitage 2004). It is now well established that growth rates of many raptor populations are highly sensitive to changes in survival rates (Stahl and Oli 2006; Krüger et al. 2010; Wootton and Bell 1992; Hiraldo et al. 1996), especially of adult breeders (Hunt 1998). Thus, rigorous estimates of survival rates and an understanding of factors influencing those rates are necessary first steps towards formulating or implementing conservation plans for Sooty Falcons, a Near Threatened species of raptor with a limited and patchy geographic distribution. Although accurate estimates of population size do not currently exist for the Sooty Falcon, available evidence suggests declining population trends (BirdLife International 2015). Data on population ecology are lacking for this species; no estimates of survival or breeding probabilities have been made previously. We sought to fill this knowledge gap.

Consistent with other avian species (e.g., Stahl and Oli 2006; Oli et al. in press), annual survival of pre-breeders was lower than that of breeders. However, 95 % confidence intervals for these rates overlapped (pre-breeders 0.282–0.616; breeders 0.510–0.778), suggesting a lack of statistical evidence for stage-specificity in apparent survival rates. We note that estimates of survival reported here are of apparent (rather than true) survival, and the loss includes both mortality and permanent emigration; thus, true survival, especially of pre-breeders (dispersing stage) would be higher than those reported here. We were unable to estimate survival in the first-year (juvenile) because birds ringed as juveniles were not encountered again until they returned as breeding adults, but analysis of survival time of radio-tagged Sooty Falcons suggests that juvenile survival is probably very low.

Only one of the five falcons tracked by satellite was recovered, but the cause of death could not be conclusively determined. Two juveniles from Oman were tracked via satellite in 2010 (Gschweng 2015), and one was tracked from Abu Dhabi, UAE (S. Javed, personal communication). Details of the fate are known for only one of the falcons radio-tagged in Oman: it was shot in the Democratic Republic of Congo during its first migration. The other juvenile from Oman apparently died soon after reaching Madagascar, and the bird from Abu Dhabi apparently died in Sudan. Additionally, none of the radio-tagged birds in this or other studies died while in their natal areas, and only two survived to reach the wintering grounds, further suggesting that mortality in juvenile Sooty Falcons occurs mostly while en route to wintering grounds. First migration may be especially perilous for Sooty Falcons because prey may be scarce, juvenile falcons are inexperienced hunters, and falcons are sometimes killed by humans. Our finding that first migration appears to be particularly lethal agrees with those of Strandberg et al. (2009) and Fiuczynski (1978) for Eurasian Hobbies (*F. subbuteo*) and Mihoub et al. (2010) for Lesser Kestrel (*F. naumanni*). Klaassen et al. (2014) found raptor mortality during migration between Europe and Africa to be higher than settled periods on breeding and wintering grounds, though that study was for adults. These data and the threats on the breeding grounds (e.g., human development of nesting islands) and on the wintering grounds (e.g., agricultural pesticides) highlight the importance of a flyway-scale approach to Sooty Falcon conservation.

The causes of death of six of the seven juveniles tracked from Oman are unknown (Table 2). Newton (2008) points out that a major cost of migration in birds is the associated mortality, but that in the long term this cost must be more than compensated for by the overall fitness benefits of migration. We could not be certain that cessation of transmissions from a moving transmitter meant that a bird had died. Some transmitters could have dropped off or malfunctioned. However, information from the sensors on board the transmitters did not indicate that there were electronic failures, and we believe that the tags would have been difficult for the birds to remove. In addition to factors identified by Newton (2008) (e.g., weather, collisions), starvation due to lack of hunting skills and experience, exacerbated perhaps by local conditions (e.g., periods of poor weather, low densities of prey in some areas) is also a possibility. Reduced body condition due to lack of food may also make juvenile falcons more susceptible to mortality factors.

The mortality rate of juveniles, if one assumes that all downed tags were due to the death of the falcon, was in line with what the ringing data suggested (although we could not estimate juvenile mortality directly from ringing). However, although the transmitters were small and within the weight constraints typically applied to birds (Kenward 2001), we could not rule out the possibility that the tags had a negative effect on survival, and subsequent tracking of five adults by us and earlier tracking of two adults by Javed et al. (2012) do not rule out the possibility of a transmitter-related increase in mortality. We cannot discount the possibility that the backpack transmitters used in our study did not contribute to the high mortality we observed, and we believe smaller transmitters are to be preferred.

On a national scale, our limited data suggest that many falcons breeding in Oman return, if they survive, but the lack of ringing and recaptures from elsewhere obscure the real rate of breeder fidelity. At a smaller scale, if one considers the nine geographically close Daymaniyat Islands and Fahal Island as two distinct breeding sites, then Sooty Falcons showed 100 % fidelity to their breeding site. For the most part, breeding Sooty Falcons also appeared to show fidelity to their territories, though some birds did move from one breeding territory to another. The inaccessibility of nests undermined our ability to estimate precisely the rate of fidelity by breeders.

Conclusions about the rate of natal philopatry are more difficult to make because no ringing efforts were being made and no ringed birds were encountered outside our study area, and pre-breeder mortality was proportionally high. In addition, Oman is on the margin of the species' breeding distribution and distant from other breeding concentrations, which are mostly in the Red Sea region. When birds ringed as juveniles in Oman did return to breed, 77 % of them bred on exactly the same island on which they were raised, but there was also some natal dispersal between the Daymaniyat Islands and Fahal.

Most raptors tend to return to the area in which they were reared, and return year after year to breed in the same home range (Newton 1979); Eleonora's Falcon (Ristow et al. 1979, 1989; Ristow 2010; Gangoso et al. 2013), and Lesser Kestrel (Mihoub et al. 2010) also appear to have very high rates of natal philopatry and nesting site fidelity. Such high rates of fidelity highlight the important role that national-level (or even colony-level) conservation efforts can play, especially in countries that hold significant populations (e.g., Egypt, Eritrea, Oman, and Saudi Arabia). On the other hand, juveniles dispersing to other breeding areas (at a presumed rate of 23 %; 1.00–0.77 natal fidelity in our study area), could contribute to the recovery and support of declining populations (e.g., Bahrain, UAE), although it is important to note that the 23 % value assumes no mortality amongst dispersing birds, which is probably not the case.

Caution must be exercised when comparing survival rates among species. However, no estimates of survival exist for Sooty Falcons from anywhere else in their geographic range, so comparison with ecologically similar falcon species is reasonable. The Sooty Falcon is most closely related to Eleonora's Falcon and Eurasian Hobby (*F. subbuteo*); Red-footed (*F. vespertinus*) and Amur Falcons (*F. amurensis*) belong to a sister genetic cluster (Wink and Ristow 2000). All these are small–medium falcons that hunt primarily aerial prey (birds and insects), undertake long-distance migrations from breeding areas in Eurasia to non-breeding areas in sub-Saharan Africa. Ecologically, Sooty Falcons and Eleonora's Falcon are most similar in that they both nest in the boreal summer so as to feed their offspring on birds migrating between Eurasia and Africa, sometimes nest in dense aggregations on islands, and most spend the non-breeding season in Madagascar. Lesser Kestrel is more distantly related to Sooty Falcons (Helbig et al. 1994), but is similar in size, is a long-distance migrant between Eurasia and Africa that feeds on insects and birds, and breeds colonially.

Using data from resightings of color-ringed individuals, Wink et al. (1987) and Ristow et al. (1989) estimated survival of Eleonora's Falcon to be 22 % for first-year birds and 86.8 % for adults. For Lesser Kestrels, first-year survival has been variously estimated at 34 % (Hiraldo et al. 1996), 57 % (Prugnolle et al. 2003) and 71 % (Mihoub et al. 2010), and adult survival has been estimated at 67 % (Prugnolle et al. 2003) and 71 % (Hiraldo et al. 1996). In addition, 72 % of Lesser Kestrels ringed as fledglings returned to their natal area after one year and an estimated 53 % of those bred in their first year. Because Sooty Falcons that were ringed and released as juveniles were never encountered until they returned to the study site as breeding adults, we could not directly estimate age-specific survival for the pre-breeders. However, annual pre-breeder survival rate of 57 % and breeding adult survival rate of 66 % estimated in this study fall within the ranges reported for ecologically similar species. We could not test for differences in survival between sexes, nor could we discern drivers of spatial and temporal variation in survival, due to data limitation. Longer-term monitoring of the population over a broader geographical range is needed to gain a more comprehensive understanding of factors and processes governing spatial and temporal variation in Sooty Falcon survival.

Many falcons of size similar to Sooty Falcon (e.g., European Kestrel *F. tinnunculus*, Merlin *F. columbarius*, Eurasian Hobby, Eleonora's Falcon) have been recorded as pairing, and successfully breeding in their first year (Newton 1979; Wink et al. 1987). Breeding by younger birds is most common when food is plentiful and nest sites available (Village 1990; Newton 1991), when populations are growing, or where adult mortality is high (Newton 1979, 1998). We observed 223 breeding pairs of Sooty Falcons for which we could age both members of the pair; we found no evidence that juvenile Sooty Falcons breed, and amongst the breeders we captured only four were 2 years of age. Mean age at first breeding is not commonly reported in raptors. However, our estimate of average age of first breeding appears similar to that for comparable falcon species (e.g., Wink et al. 1987; Ristow et al. 1989; Hiraldo et al. 1996; Prugnolle et al. 2003). Age of first breeding in Peregrine Falcon (*F. peregrinus*) (which are larger and live longer than Sooty Falcon, and also have only a single non-adult plumage) can range from 2–4 years, depending on stage of population growth and local environmental conditions (Ratcliffe 1980; Tordoff and Redig 1997; Zuberogoitia et al. 2009),

Age of first breeding is an important life-history trait that can influence fitness, and may affect the ability of a population in decline to recover (Cole 1954; Roff 1992; Oli and Dobson 2003). The trade-off between age of first breeding and lifetime reproductive success suggests that, for each species and in each situation, an optimal age of first breeding exists (Roff 1992; Krüger 2005). Age of first breeding can also serve as a good early-warning signal of population decline for raptors, with delayed age of first breeding indicating impending population declines (Balbontin et al. 2003; Zuberogoitia et al. 2009). Our results suggest that Sooty Falcons are capable of breeding at 2 years of age, but that breeding may be delayed substantially depending perhaps on the environmental conditions.

Keeping in mind that the processes that have the biggest effect on factors that affect survival might act on flyway (e.g., prey bird migration patterns) or global scales (e.g., climate that might affect avian and insect prey numbers and availability), one way of improving survival of juvenile Sooty Falcons would be to implement conservation measures on their migration route, where the majority of juvenile mortality seems to occur. Bird Life International's Migratory Soaring Bird Project (http://www.migratorysoaringbirds.undp.birdlife.org/) and CMS's Raptor MOU (http://www.cms.int/raptors/en/page/agreement-text) are initiatives that highlight both the importance and the difficulty of tackling conservation of migratory raptors, like the Sooty Falcon, along the Africa–Eurasia Flyway. Implementation of conservation measures in poor countries is challenging, but can be successful. For example, public conservation education efforts in extremely poor areas of India, where Amur Falcons were being killed in large numbers, seem to be quickly gaining momentum and having an effect (See: http://www.birdlife.org/asia/news/action-amur-falcons-brings-hope-end-hunting-nagaland).

Survival is an influential demographic parameter with substantial potential to influence dynamics and persistence of raptor and many other avian populations (Hiraldo et al. 1996; Stahl and Oli 2006). Unfortunately, estimates of population growth rate or quantification of sensitivity/elasticity of population growth rate to vital demographic parameters (Caswel 2001) are currently not available for Sooty Falcons. Although our study has provided the first estimates of state-specific apparent survival and age-specific breeding probabilities, our understanding of Sooty Falcon ecology remains poor. Similar studies in other parts of the Sooty Falcon's breeding range, particularly around the Red Sea, would allow comparison of survival and breeding probabilities among populations breeding in different sites. Because of relatively low recapture rates, we could not test for temporal variation in survival, recapture or breeding probabilities, or statistically compare these parameters between the two island chains. Color ringing has been successfully used to collect data on turnover and survival for Eleonora's Falcon (Ristow et al. 1991), and can help improve recapture rates (and, thus, effective sample size), and should be considered (in conjunction with breeding season field work occurring throughout the time falcons are present) in future work on this species, especially on islands were breeders aggregate. While PIT ringing did have the advantage of 100 % positive identification of ringed birds that were nesting, it did not permit us to identify ringed birds unless they were nesting and we could access their nests. Consequently, marked birds that nested in inaccessible places or did not nest at all largely went undetected.

We were unable to tease apart losses from mortality and those from permanent emigration or dispersal because no substantial ringing efforts were made at other breeding sites, and only one bird fitted with a transmitter was recovered. Teasing apart death and dispersal, and discerning timing and causes of mortality, would require radio-tracking of a fairly large number of birds, tracking their fates via satellite and on-the-ground investigation of birds suspected to have died (Williams et al. 2001). Finally, this study provides information on Sooty Falcon survival rates and breeding probabilities, which are only two of several life-history traits that determine population dynamics and persistence, and important gaps exist. For example, aspects of reproductive ecology of Sooty Falcons are currently poorly understood, though we aim to start filling that knowledge gap by reporting data on occupancy and productivity for Sooty Falcons breeding in Oman. Sooty Falcon conservation efforts would greatly benefit from a comprehensive understanding of the species' population dynamics and persistence using realistic and empirically-based estimates of demographic parameters, with due attention to factors that would introduce variability and uncertainty.

Acknowledgments Financial support was provided by the Office for Conservation of the Environment Diwan of Royal Court (OCE), Natural Research, Ltd., UK, Petroleum Development Oman and the Environment Society of Oman. In-kind and logistical support was provided by the Royal Yachts of Royal Court Affairs and the Ministry of Environment and Climate Affairs (MECA). Research permits for the Daymaniyat Islands were kindly provided by MECA, and permission to land on Fahal Island by the Royal Oman Police. We would particularly like to thank the captains and crew of the "Al Noores" and the MECA rangers for their hospitality and logistical support. The Environment Society of Oman provided some PIT tag reading equipment. Many individuals were very helpful including: Y. Al-Salami, A. Spalton, M. Al-Balushi, A. Al-Owisi, N. Al-Sharji, A. Al-Amri, A. Al-Raisi, J. Knapp, A. Al-Kyumi, F. Al-Lamki, K. Am Busaidi, M. Hearst, R. Eaton, M. Nicoll, A. Thorpe, M. Gschweng, L. Arison and G. Razafimanjato. A. Al-Raisi provided GIS support. The help provided by Said Al-Sayabi of the Royal Yachts was vital to the success of the work. The manuscript was greatly improved by the comments of two anonymous referees. Finally, we are immensely grateful to James D. Nichols for much needed guidance in data analysis. The work was performed in accordance with the laws of the Sultanate of Oman.

References

Balbontin J, Penteriani V, Ferrer M (2003) Variations in the age of mates as an early warning signal of changes in population trends? The case of Bonelli's Eagle in Andalusia. Biol Conserv 109:417–423

BirdLife International (2015) Species factsheet: *Falco concolor*. http://www.birdlife.org. Accessed 2 Feb 2015

Caswel H (2001) Matrix population models: construction, analysis, and interpretation. Sinauer, Sunderland

Cole LC (1954) The population consequences of life history phenomena. Q Rev Biol 29:103–137

Del Hoyo J, Elliott A, Sargatal J (1994) The handbook of birds of the world, vol 2. Lynx, Barcelona

Evans MI (1994) Important bird areas in the Middle East. BirdLife International, Cambridge

Ferguson-Lees J, Christie DA (2001) Raptors of the world. Black, London

Fiuczynski D (1978) Zur Populationsökologie des Baumfalken (*Falco subbuteo* L., 1758). Zool Jb Syst 105:193–257

Frumkin R (1988) Biologie und Bestimmung des Schieferfalken *Falco concolor*. Limicola 2:83–109

Frumkin R (1993) Breeding ecology of the Sooty Falcon in Israel. In: Nicholls MK, Clark R (eds) Biology and conservation of small falcons. Proceedings of.Hawk and Owl Trust Conference, 6–8 September 1991, Canterbury, pp 51–58

Frumkin R, Pinshow B (1983) Notes on the breeding ecology and distribution of the Sooty Falcon *Falco concolor* in Israel. Ibis 125:251–259

Gangoso L, López-López P, Grande JM, Mellone U, Limiñana R, Urios V, Ferrer M (2013) Ecological specialization to fluctuating resources prevents long-distance migratory raptors from becoming sedentary on islands. PLoS ONE 8(4):e61615

Gaucher P, Petit T, Symens P (1988) Notes on the study of the Sooty Falcon (*Falco concolor*) during its breeding season in Saudi Arabia. Alauda 56:277–283

Gaucher P, Thiollay J-M, Eichaker X (1995) The Sooty Falcon (*Falco concolor*) on the Red Sea coast of Saudi Arabia: distribution, numbers and conservation. Ibis 137:29–34

Gosler A (2004) Birds in the hand. In: Sutherland WJ, Newton I, Green RE (eds) Bird ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, pp 85–118

Gschweng M (2015) http://Sootyfalconoman.blogspot.co.at/. Accessed 24 March 2015

Gschweng M, Kalko EK, Querne U, Fiedle W, Berthold P (2008) All across Africa: highly individual migration routes of Eleonora's Falcon. Proc R Soc Lond B 275(1653):2887–2896

Helbig AJ, Seibold I, Bednarek W, Gaucher P, Ristow D, Scharlau W, Wink M (1994) Phylogenetic relationships among falcon species (genus *Falco*) according to DNA sequence variation of the cytochrome b gene. In: Chancellor RD, Meyburg B-U (eds) Raptor conservation today. Pica and WWGBP, London, pp 593–599

Hiraldo F, Negro JJ, Donázar JA, Gaona P (1996) A demographic model for a population of the endangered Lesser Kestrel in southern Spain. J Appl Ecol 33:1085–1093

Hunt WG (1998) Raptor floaters at Moffat's equilibrium. Oikos 82:191–197

Javed S, Douglas DC, Khan S, Shah JN, AlHammadi AA (2012) First description of autumn migration of Sooty Falcon *Falco concolor* from the United Arab Emirates to Madagascar using satellite telemetry. Bird Conserv Int 22:106–119

Kavanagh B, King H (2008) Observations from 1998–2006 on the breeding population of Sooty Falcons *Falco concolor* on the Hawar Islands, Kingdom of Bahrain. Sandgrouse 30:70–76

Kenward RE (2001) A manual for wildlife radio tagging. Academic, London

Klaassen RH, Hake M, Strandberg R, Koks BJ, Trierweiler C, Exo K-M, Bairlein F, Alerstam T (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. J Anim Ecol 83:176–184

Krüger O (2005) Age at first breeding and fitness in Goshawk *Accipiter gentilis*. J Anim Ecol 74:266–273

Krüger O, Grünkorn T, Struwe-Juhl B (2010) The return of the White-tailed Eagle (*Haliaeetus albicilla*) to northern Germany: modelling the past to predict the future. Biol Conserv 143:710–721

Laake J, Rextad E (2015) RMark–an alternative approach to building linear models in MARK. In: Cooch E, White GC (eds) MARK: a gentle introduction. http://www.cnr.colostate.edu/~gwhite/mark/mark/html, pp C1–C115

Lebreton JD, Hines JE, Pradel R, Nichols JD, Spendelow JA (2003) Estimation by capture-recapture of recruitment and dispersal over several sites. Oikos 101:253–264

López-López P, Liminana R, Mellone U, Urios V (2010) From the Mediterranean Sea to Madagascar: are there ecological barriers for the long-distance migrant Eleonora's Falcon? Landscape Ecol 25:803–813

McGrady MJ, Nicoll MAC (2008) A study of the status and distribution of breeding Sooty Falcons (*Falco concolor*) on the northern islands of Oman–2007 and 2008. Unpublished report, Office of Conservation of the Environment, Muscat

Mihoub J-B, Giménez O, Pillard P, Sarrazin F (2010) Challenging conservation of migratory species: sahelian rainfalls drive first-year survival of the vulnerable Lesser Kestrel *Falco naumanni*. Biol Conserv 143:839–847

Newton I (1979) Population ecology of raptors. Poyser, London

Newton I (1991) The role of recruitment in population regulation. Proc Int Ornithol Congr 20:1689–1699

Newton I (1998) Population limitation in birds. Academic, London

Newton I (2008) The migration ecology of birds. Academic, London

Oli M, Armitage K (2004) Yellow-bellied Marmot population dynamics: demographic mechanisms of growth and decline. Ecology 85:2446–2455

Oli MK, Dobson FS (2003) The relative importance of life-history variables to population growth rate in mammals: cole's prediction revisited. Am Nat 161:422–440

Oli MK, McGrady MJ, Murillo-García O, Nichols JD, Newton I (in press) Patterns in raptor survival estimates. Ibis

Pollock KH, Winterstein SR, Bunck CM, Curtis PD (1989) Survival analysis in telemetry studies: the staggered entry design. J Wildl Manag 53:7–15

Porter R, Aspinall S (2010) Birds of the Middle East. Christopher Helm, London

Prugnolle F, Pilard P, Brun L, Tavecchia G (2003) First-year and adult survival of the endangered Lesser Kestrel *Falco naumanni* in southern France. Bird Study 50:68–72

Ratcliffe D (1980) The Peregrine Falcon. Poyser, Berkhamsted

Ristow D (2010) Up-date on breeding status and review on Eleonora's Falcon (*Falco eleonorae*) when away from the breeding sites. Il Merill 32:1–5

Ristow D, Wink C, Wink M (1979) Site tenacity and pair bond of Eleonora's Falcon. Il Merill 20:16–18

Ristow D, Scharlau W, Wink M (1989) Population structure and mortality of Eleonora's Falcon *Falco eleonorae*. In: Meyburg B-U, Chancellor RD (eds) Raptors in the modern world. WWGBP, London, pp 321–326

Ristow D, Feldmann F, Scharlau W, Wink C, Wink M (1991) Population dynamics of Cory's Shearwater (*Calonectris diomedea)* and Eleonora's Falcon (*Falco eleonorae*) in the eastern Mediterranean. In: Loeschcke V, Seitz E (eds) Species conservation: a population-biological approach. Birkhauser, Basel, pp 199–212

Roff DA (1992) The evolution of life histories. Chapman and Hall, New York

Semere D, Hagos T, Seleba G, Gebrezgabhier Y, Haile Z, Chiozzi G, De Marchi G (2008) The status of breeding seabirds and water birds on the Eritrean Red Sea islands. ABC Bull 15:228–237

Shah JN, Khan SB, Ahmed S, Javed S, AlHammadi A (2008) Sooty Falcon in the United Arab Emirates. Falco 32:16–19

Smith GD, McGrady MJ (2009) Using passive integrated transponder (PIT) tags to better understand a Peregrine Falcon (*Falco peregrinus*) population in south Scotland and north east England. In: Sielicki J, Mizera T (eds) Peregrine Falcon populations—status and perspectives in the 21st century. Proc of workshop of the European Peregrine Falcon Working Group, Society for the protection of wild animals, Turul, Warsaw, pp 245–258

Spendelow JA, Nichols JD, Hines JE, Lebreton JD, Pradel R (2002) Modelling post fledging survival and age-specific breeding probabilities in species with delayed maturity: a case study of roseate terns at Falkner Island, Connecticut. J App Stat 29:385–405

Stahl JT, Oli MK (2006) Relative importance of avian life-history variables to population growth rate. Ecol Model 198:3–39

Strandberg R, Klaassen RH, Hake M, Alerstam T (2009) How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. Biol Lett. doi:10.1098/rsbl.2009.0785

Tordoff HB, Redig PT (1997) Midwest peregrine falcon demography, 1982–1995. J Raptor Res 31:339–346

Village A (1990) The kestrel. Poyser, London

Walter H (1979a) The Sooty Falcon (*Falco concolor*) in Oman: results of a breeding survey. J Oman Studies 5:9–59

Walter H (1979b) Eleonora's Falcon: adaptations to prey and habitat in a social raptor. University of Chicago Press, Chicago

White GC, Burnham KP (1999) Program MARK: survival rate estimation from both live and dead encounters. Bird Studies 46(Suppl):S120–S139

Williams BK, Nichols JD, Conroy MJ (2001) Analysis and management of animal populations. Academic, San Diego

Wink M, Ristow D (2000) Biology and molecular genetics of Eleonora's Falcon *Falco eleonorae*, a colonial raptor of Mediterranean islands. In: Chancellor RD, Meyburg B-U (eds) Raptors at risk. WWGBP/Hancock House, Berlin, pp 653–668

Wink M, Scharlau W, Ristow D (1987) Population structure in a colony of Eleonora'S Falcon (*Falco eleonorae*). Suppl Ric Biol Selvaggina 12:301–305

Wootton JT, Bell DA (1992) A metapopulation model ofthe peregrine falcon in California: viability and managementstrategies.Ecol Appl2:307–321

Zuberogoitia I, Martínez JA, Azkona A, Marínez JE, Castillo I, Zabala J (2009) Using recruitment age, territorial fidelity and dispersal as decisive tools in the conservation and management of peregrine falcon (*Falco peregrinus*) populations: the case of a healthy population in northern Spain. J Ornithol 150:95–101