

# Sooty Falcon *Falco concolor* reproduction and population dynamics on the islands in the Sea of Oman

MICHAEL J. MCGRADY,<sup>1\*</sup>  WAHEED A. AL-FAZARI,<sup>2</sup> MANSOOR H. AL-JAHDHAMI,<sup>2</sup> MALCOLM A. C. NICOLL<sup>3</sup> & MADAN K. OLI<sup>4</sup>

<sup>1</sup>International Avian Research, Am Rosenhügel 59, 3500 Krems, Austria

<sup>2</sup>Office of Conservation for the Environment, Diwan of Royal Court, PO Box 246, Muscat, 100, Oman

<sup>3</sup>Zoological Society of London, Regent's Park, London NW1 4RY, UK

<sup>4</sup>Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, USA

Knowledge of demographic parameters affecting population dynamics is critical to the formulation of effective conservation strategies. Sooty Falcon *Falco concolor* is a little-studied, Near-threatened species; estimates of global population size and trend for this species are uncertain. They lay eggs during mid-summer and sometimes nest in colonies. This unusual breeding ecology suggests that demographic parameters driving their population growth rate may differ from those of most other falcons. We studied Sooty Falcon reproduction at breeding aggregations on Fahal Island and the Daymaniyat islands in the Sea of Oman during 2007–2014, modelled population growth and identified important life history parameters using elasticity analysis. The mean ( $\pm$  se) clutch and brood size was  $2.83 \pm 0.06$  and  $2.11 \pm 0.07$ , respectively. Overall, 11.7% of nests failed between the egg and nestling stages, and the failure rate differed significantly between Fahal and the Daymaniyats, and across years. The mean proportion of eggs that hatched annually was  $0.66 \pm 0.02$ , and broods were significantly smaller on the Daymaniyats than on Fahal. Falcons on Fahal Island had a higher rate of hatching, a higher rate of nests that produced at least one chick, and produced more chicks per nest than on the Daymaniyats. We suggest that Fahal's proximity to the mainland gives breeding Sooty Falcons access to a more plentiful and stable source of food, especially during the period between arrival from the wintering grounds and the onset of the autumn migration of prey birds, resulting in the better reproductive rates for falcons on Fahal Island, relative to those on the Daymaniyat Islands. The annual asymptotic population growth rate ( $\lambda$ ) was 0.87 (95% confidence interval (CI) 0.75–0.99), suggesting a declining population, although Sooty Falcons enjoyed a slightly higher population growth rate on Fahal than on the Daymaniyats. Because our study population is on the edge of the breeding range and is isolated from other breeding areas, measures to improve reproductive success of Sooty Falcons breeding on the islands in the Sea of Oman could be important for conservation of Sooty Falcons in Oman.

**Keywords:** breeding success, hatching rate, Oman, population growth, reproduction, Sooty Falcon.

Adult survival is typically the main driver of population dynamics in long-lived birds (Newton 1979). However, because reproduction is an

important component of population dynamics, monitoring and understanding the causes of variation in reproductive success are important to the conservation of birds, including raptors (Newton 1998, Sæther & Bakke 2000, Stahl & Oli 2006, Steenhof & Newton 2007). Reproductive

\*Corresponding author.  
Email: mikejmcgrady@aol.com

parameters can be particularly important in driving the dynamics of populations characterized by low immigration rates (Manlik *et al.* 2016); in such populations, recruits consist primarily of individuals born or hatched within the population that survive to reproductive age.

Sooty Falcon *Falco concolor* is a globally Near-threatened species (BirdLife International 2017) that breeds in the Middle East and northeastern Africa. Breeding areas in the Arabian Gulf are distant from the main breeding area, the eastern edge of which is the Red Sea. Sooty Falcons nest singly (mostly) on the mainland, and sometimes colonially on small islands. They breed in mid-summer, and feed their growing chicks on small birds migrating in autumn from Eurasia to Arabia and Africa, a strategy shared only with Eleonora's Falcon *Falco eleonora*. The almost unique breeding strategy of this species suggests that demographic drivers of population change may differ from better-studied falcon species, and information on these may be critical for effective conservation.

BirdLife International (2017) estimates the global population of Sooty Falcons at 10 000–19 999 breeding individuals, but uncertainty surrounds this estimate (del Hoyo *et al.* 1994, Gaucher *et al.* 1995, Kavanaugh & King 2008). Keeping the uncertainty in mind, our study area on the Daymaniyat and Fahal Islands of Oman may hold 0.02–9.1% of the global population of breeding Sooty Falcons (Walter 1979b, Gaucher *et al.* 1995, M. McGrady and Office for Conservation of the Environment unpubl. data). The Convention on Migratory Species (CMS) lists Sooty Falcon as a Category 1 species under the 'Raptors MOU' initiative (Convention on Migratory Species 2008). Despite its apparently poor conservation status, little is known about population dynamics of the Sooty Falcon.

First migration can be perilous for juvenile raptors (Klaassen *et al.* 2014). Capture-mark-recapture and satellite-tracking studies suggest that survival of juvenile Sooty Falcons is low, and most juvenile deaths occur during their first outward migration towards their wintering grounds in Madagascar (McGrady & Gschweng 2011, McGrady 2014, McGrady *et al.* 2016). Information on reproduction and modelling of the population is an important step to filling knowledge gaps.

Using data from a 7-year study of Sooty Falcons breeding on the Daymaniyat and Fahal Islands of Oman (where most Sooty Falcons in

Oman breed; Walter 1979b), we aimed to: (1) provide estimates of reproductive parameters, and compare them between the island groups and across years; (2) integrate those reproductive parameters with estimates of survival rates (McGrady *et al.* 2016) to estimate population growth rate; and (3) undertake sensitivity analysis to identify life history parameters to be targeted for species conservation. The data on productivity were collected from > 200 nests during 2007–2014. The estimate of population growth is the first ever produced for this species of conservation concern. We discuss our results in the context of the late nesting characteristics of Sooty Falcons, and assess whether food availability and nearness to the mainland (Xirouchakis *et al.* 2012) may explain annual and island-group variation in reproductive parameters.

## METHODS

Sooty Falcon breeds in the Middle East and northeastern Africa; Oman, Saudi Arabia, Eritrea and Egypt are the main breeding strongholds (Gaucher *et al.* 1995, Semere *et al.* 2008). It breeds in colonies on some islands in the Red Sea and Sea of Oman and singly on the mainland, particularly in Egypt (Sinai and the southern deserts) and Israel (del Hoyo *et al.* 1994, BirdLife International 2017). Significant numbers of Sooty Falcons may breed on mainland sites, although surveys have been conducted only in Israel (M. Goren pers. comm.) and the coastal strip of the Red Sea in Saudi Arabia (Gaucher *et al.* 1995). Sooty Falcons nesting on islands constitute most of the known breeding population (Gaucher *et al.* 1995, Gallo Orsi *et al.* 2014). Oman is located on the edge of Sooty Falcon breeding range, and the nearest concentrations of more than a few breeding pairs are located > 1800 km away in the Red Sea (BirdLife International 2017). A declining population of about 10 pairs breed on the Hawar Islands in Bahrain (Kavanaugh & King 2008), which are about 800 km distant; a few pairs breed in the United Arab Emirates (Shah *et al.* 2008).

## Study area and field methods

During 2007–2014, we gathered information on Sooty Falcon presence at nesting sites and reproduction on islands in the Sea of Oman (Fig. 1): Fahal Island (23.68°N, 58.50°E), and the nine

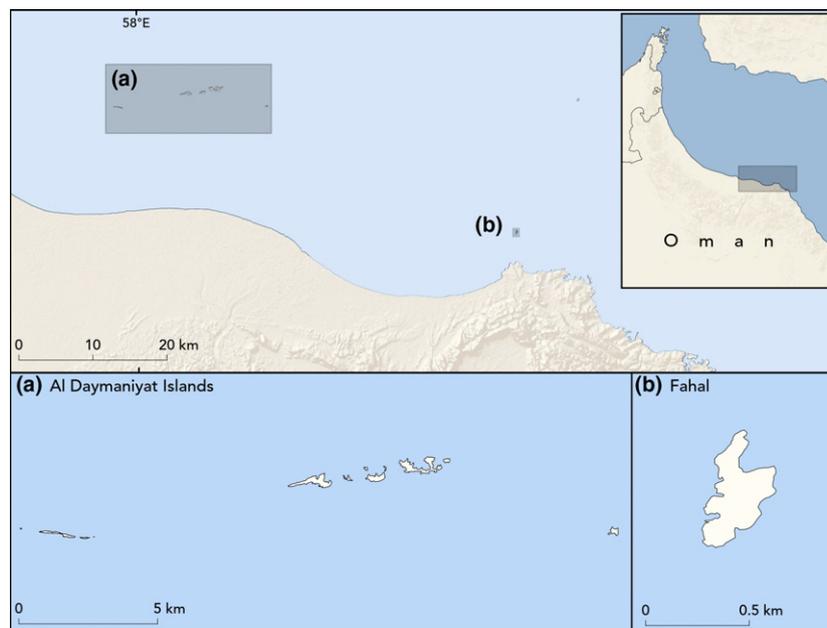
islands in the Daymaniyat archipelago (23.85°N, 58.09°E, D1 (farthest east) to D9 (farthest west)). Oman's breeding population is almost entirely found on these islands (Walter 1979b, Office for Conservation of the Environment & M. McGrady unpubl. data). The islands have been described in detail by Walter (1979b) and McGrady *et al.* (2016). The Daymaniyat Islands are a National Marine Nature Reserve; Fahal and the Daymaniyats are Important Bird Areas (Evans 1994), in Fahal's case due solely to the Sooty Falcons that breed there. During the study the nine islands in the Daymaniyat chain had 18–41 breeding pairs per year; Fahal Island had 32–41. Estimated number of pairs per island, and the number of nests that contributed to our analyses are given in Supporting Information Table S2.

In most years, two bouts of fieldwork occurred: in August, when most breeding Sooty Falcons were incubating eggs (only 1.9% of clutches were initiated after our August field work), and during September–October, when chicks were old enough to ring (Supporting Information Table S1). Fledging commenced around 5 October. We ceased fieldwork around that date because our activities could cause chicks to fledge prematurely and fall into the sea. Fieldwork was carried out

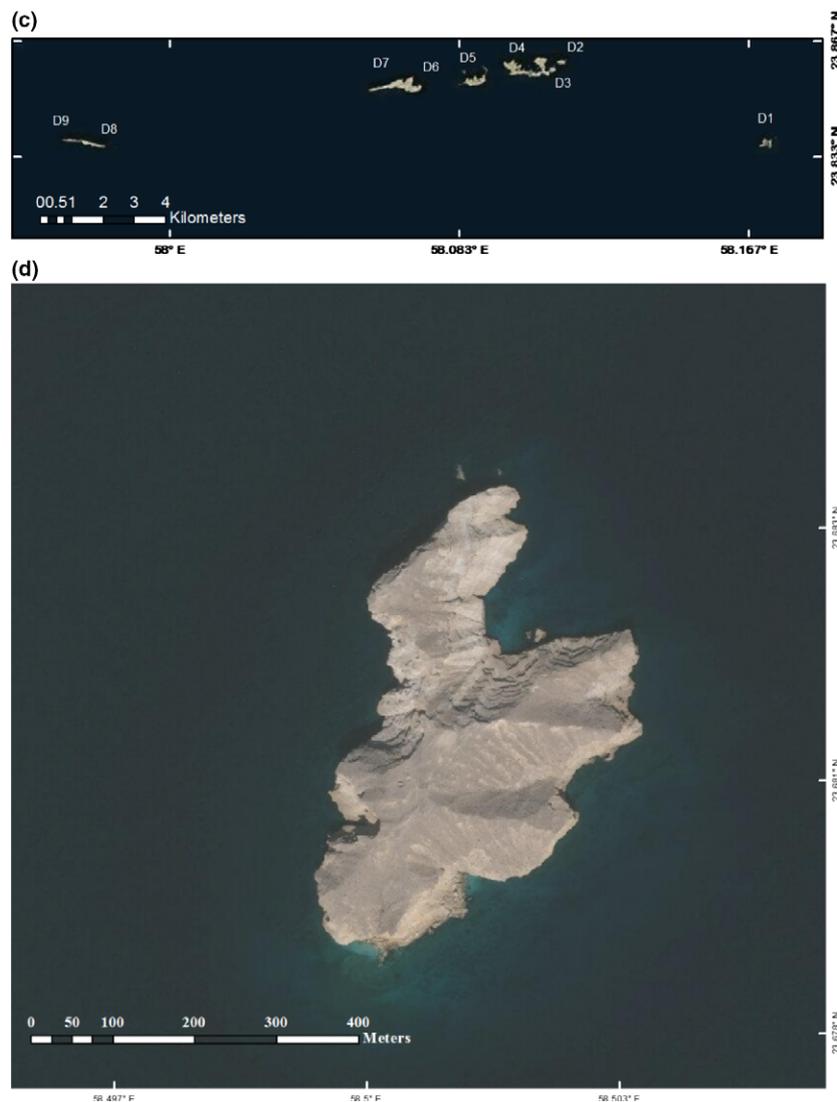
mostly in the early morning and late afternoon to avoid the heat.

We systematically searched the islands from boats and on foot for Sooty Falcons at nesting sites and their nests. Falcons were considered to be present at a nesting site if we observed at least one non-juvenile bird in attendance during July–November, or if we observed newly fledged birds during 1 October–10 November. Boat-based searches were made by one to four observers using binoculars and a boatman in 3- to 8-m motorboats; searches on foot were made by one to six observers walking along the top or bottom of cliffs and inspecting niches where falcons might nest. Some sites where falcons were present showed no signs of nesting (inattentive adults, no scrape, eggs or chicks found).

Using the presence of attendant Sooty Falcons as evidence of possible nesting, we searched all accessible areas of the islands with the aim of finding as many nests as possible. Most nests were accessed without the use of climbing equipment. Areas of the islands that were inaccessible were searched using binoculars from the land or a boat but, some areas, especially on Fahal, could not be accessed or viewed from either land or sea. At accessible nests we determined whether they were



**Figure 1.** Map of the study area. Inset: regional map. Upper panel: location of Daymaniyat Islands (a) and Fahal Island (b) to north Oman coast. Lower panel: zoomed maps of Daymaniyat Islands (a) and Fahal Island (b). [Colour figure can be viewed at [http://onlinelibrary.wiley.com/journal/10.1111/\(ISSN\)1474-919X](http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1474-919X)]



active (containing at least one egg) in August, and productive (rearing at least one young to ringing age) in September–October, recording the actual number of eggs and the number of chicks to reach ringing age (over about 10–12 days) at each nest.

In August we captured breeders and ringed them (McGrady *et al.* 2016). In September–October, besides revisiting the nests we had found in August to record the number of chicks, we also searched for nests we had failed to locate in August. We recorded the number of chicks in these newly found nests, and ringed all chicks in accessible nests. We report means  $\pm$  1 se for reproductive parameters.

### Statistical analysis

We considered four variables related to Sooty Falcon productivity in our analyses: clutch size (number of eggs per nest), brood size (number of chicks of ringing age per nest), hatching success rate (number of chicks hatched per egg counted at nests; also incorporates pre-ringing chick mortality), and nesting success rate (proportion of nests with at least one egg that produced at least one chick of ringing age). For the analysis of clutch size, we excluded all observations with incomplete egg counts. Likewise, our analysis of the number of chicks produced per nest was based only on

observations with complete chick counts. To test for the difference in clutch size and chick production between the two island chains (Daymaniyat and Fahal), we used generalized linear mixed models (GLMMs; Zuur *et al.* 2009, Agresti 2015) with Poisson distribution and log-link, and random effect of year and nest-site because some of the nest-sites were sampled in two or more years. We considered a nesting attempt to be productive (coded 1) if it produced at least one chick during a nesting season; otherwise it was considered failed (coded 0). We considered GLMMs with binomial distribution and logit-link and random effect of year and nest-site to test for the difference in hatching success rate and nesting success rate between the two island chains. Finally, we also tested for year-to-year differences in reproductive parameters by treating year as a fixed effect factor covariate, and for temporal trend by treating year as a fixed effect continuous covariate; nest-site was included as a random effect in these analyses. We used R package *lme4* to fit GLMMs (Bates *et al.* 2016); all other statistical analyses were performed using the R computing environment (R Core Team 2014). Maps were produced using QGIS desktop (ver. 2.6, QGIS 2014).

#### Demographic analysis

We constructed and analysed female-only, age-structured matrix population models, with four age classes (Caswell 2001). From fledging to age class 2, birds survive with annual juvenile survival probability  $P_j$  and with annual adult survival probability  $P_a$  thereafter. We used estimates of survival of birds prior to breeding (dispersing age class) and breeding birds (McGrady *et al.* 2016) as surrogates for juvenile and adult survival. Reproduction begins at age 2, and birds reproduce with age-specific fertility rates,  $F_i$ . The age-structured population projection matrix was of the form:

$$A = \begin{bmatrix} 0 & F_2 & F_3 & F_4 & F_5 \\ P_j & 0 & 0 & 0 & 0 \\ 0 & P_j & 0 & 0 & 0 \\ 0 & 0 & P_a & 0 & 0 \\ 0 & 0 & 0 & P_a & P_a \end{bmatrix}$$

where  $F_i$  is age-specific fertility rate calculated using the post-breeding census method, and assuming a 50 : 50 sex ratio (Caswell 2001):

$$F_i = \begin{cases} P_j \Psi_i \gamma^{*0.5}, & \text{for } i = 2 \\ P_a \Psi_i \gamma^{*0.5}, & \text{for } i > 2 \end{cases}$$

where  $\gamma$  is the average number of chicks produced by a breeding pair per year and  $\Psi_i$  is the age-specific breeding probability. The structure of our demographic model was dictated by the species' biology and data availability. Sooty Falcons that are ringed as hatchlings are not encountered again until they return as breeders; only about 4% of falcons ringed as hatchlings returned to our study site as breeders (McGrady *et al.* 2016). Consequently, it was not possible to estimate age-specific estimates of survival for pre-breeders; thus, our estimate of  $P_j$  represents average annual survival for the pre-reproductive stage. Furthermore, we did not have data-based estimates of age of last reproduction; available data did not permit estimation of age-specific demographic parameters for ages  $> 4$  years.

We estimated  $\gamma$  as the number of chicks hatched per nest per year, considering only nests with complete chick counts.  $P_j$ ,  $P_a$  and  $\Psi_i$  were estimated using multistate capture-mark-recapture methods (Williams *et al.* 2001, Lebreton *et al.* 2003); methodological details are given in McGrady *et al.* (2016). Using the population projection matrix thus parameterized (see Table 1 for parameter values), we followed Caswell (2001) to estimate deterministic finite population growth rate ( $\lambda$ ), stable stage distribution, reproductive values, age-specific life-expectancy and the proportional sensitivity (elasticity) of  $\lambda$  to lower-level vital rates. The delta method was used to estimate variance and confidence intervals of  $\lambda$  (Caswell 2001). Variances of  $P_j$ ,  $P_a$  and  $\Psi_i$  were estimated using multistate capture-mark-recapture models, and variance of  $\gamma$  was estimated as the temporal variance of the number of hatchlings produced (i.e. random effect of year on the number of hatchlings).

Survival probabilities estimated using the capture-mark-recapture methods are apparent, rather than true, survival because losses include both death and natal dispersal (Williams *et al.* 2001). Consequently, survival of dispersing age classes is underestimated, which also leads to underestimation of  $\lambda$ . Because we did not have data-based estimates of natal dispersal rates, we assumed that dispersal occurs predominantly during the first

**Table 1.** Estimates of demographic parameters (mean  $\pm$  sd) used to parameterize the matrix population model. Demographic  $P_j$ ,  $P_a$  = survival of juveniles and adults;  $\psi_i$  = breeding probability of age class  $i$ ;  $\gamma$  = productivity (number of chicks produced per breeding pair). Survival and breeding probabilities were estimated by McGrady *et al.* (2016).

Parameter	Estimate
$P_j$	0.570 $\pm$ 0.048
$P_a$	0.656 $\pm$ 0.069
$\Psi_2$	0.065 $\pm$ 0.036
$\Psi_3$	0.159 $\pm$ 0.069
$\Psi_4$	0.339 $\pm$ 0.211
$\gamma$	2.110 $\pm$ 0.048

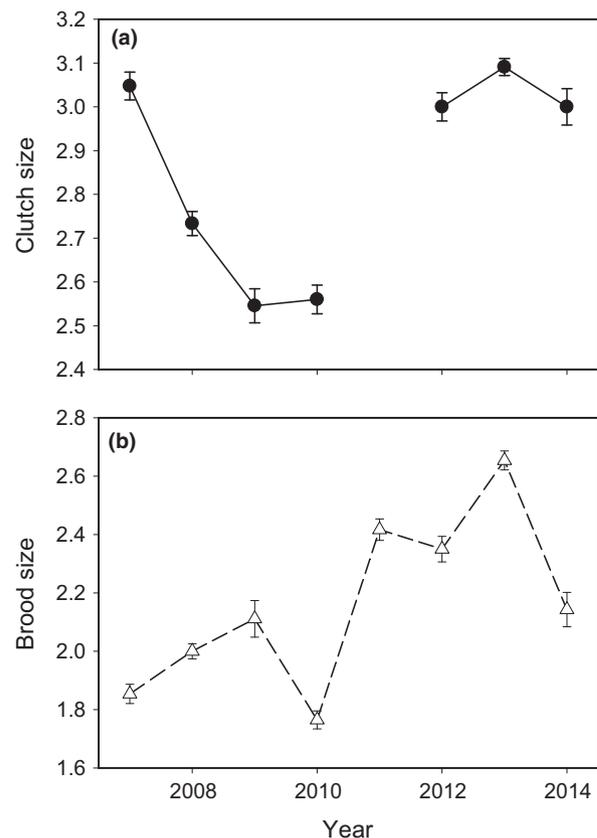
year of life, and calculated  $\lambda$  for a range of natal dispersal rates.

## RESULTS

### Productivity

Overall, clutches comprised a mean of  $2.83 \pm 0.06$  eggs per nest ( $n = 153$ , range: 1–4); 83 were three-egg clutches. Mean clutch size was  $2.92 \pm 0.08$  on the Daymaniyats ( $n = 100$ ) and  $2.66 \pm 0.08$  on Fahal ( $n = 53$ ). Annual mean egg production varied between 2.40 (2009) and 3.27 (2014) on the Daymaniyats, and between 2.50 (2014) and 2.90 (2013) on Fahal (Figs 2 & 3). There was no difference in clutch size between Fahal and the Daymaniyats ( $z = -0.908$ ,  $P = 0.364$ ). Random effects of year and nest location were both close to zero, indicating no substantial variation in clutch size among nest locations or across years. There was no evidence for year-to-year difference in clutch size ( $P > 0.320$ ) or for temporal trend ( $\beta = 0.013 \pm 0.024$ ,  $P = 0.601$ ).

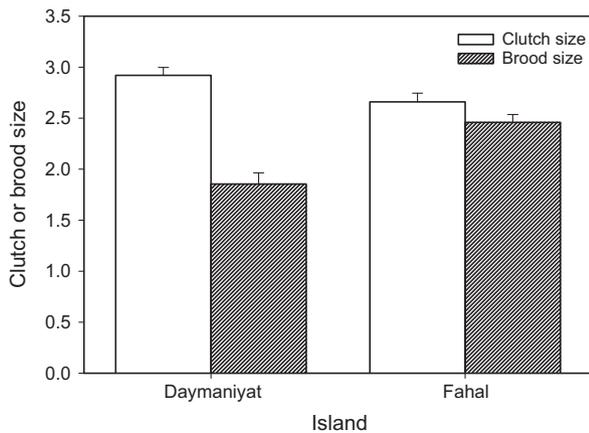
During the study period, 30 of 256 (11.7%) nests failed between our visits during the egg stage and our visits during the nestling stage. Nest failure was highest in 2007 (26.7%) and lowest in 2011–2013, when no nests failed. Nest failures in 2007 accounted for 40% (12 of 30) of all nest failures between visits. On the Daymaniyat Islands, chicks were found in 80.3% of the nests that had eggs; on Fahal in 99.1%. Nesting success rate differed between Fahal and the Daymaniyats ( $z = 3.251$ ,  $P = 0.001$ ); the random effect of year was substantial (variance = 1.211), suggesting substantial temporal variation in nesting success; the



**Figure 2.** The average ( $\pm 1$  se) clutch size (a) and brood size (b) for Sooty Falcons in Oman for each year of the study (2007–2014). Nests with incomplete egg or chick counts were not included in calculations. Clutch size was not determined in 2011.

random effect of nest location was practically zero. There was no evidence for year-to-year differences in nesting success ( $P > 0.05$ ). There was an increasing trend in nesting success over time ( $\beta = 0.298 \pm 0.100$ ,  $P = 0.003$ ).

On average,  $66.4 \pm 1.8\%$  of eggs hatched annually, but hatching success rate varied between 37.7% (2007) and 79.3% (2013). Hatching success rate differed between Fahal and the Daymaniyats ( $z = 4.389$ ,  $P < 0.001$ ), with 54.5% of eggs hatched on the Daymaniyat Islands and 87.9% on Fahal. The random effects of nest-site (variance = 1.904) and year (variance = 0.254) were both substantial, suggesting significant variation in hatching success among nests and across years. Year-to-year differences in hatching success were significant ( $P < 0.05$ ), with hatching success in 2007 being lower than in all other years, except 2014. However, there was no evidence of a



**Figure 3.** The average ( $\pm 1$  se) clutch and brood size for Sooty Falcons nesting on Fahal and the Daymaniyat Islands in Oman.

temporal trend in hatching success ( $\beta = 0.118 \pm 0.082$ ,  $P = 0.152$ ).

Mean brood size was  $2.11 \pm 0.074$  per active nest (nests  $\geq$  one egg,  $n = 226$ ); it ranged from  $1.76 \pm 0.031$  in 2010 to  $2.65 \pm 0.0325$  in 2013. The mean was  $1.85 \pm 0.01$  ( $n = 130$ ) on the Daymaniyats and  $2.45 \pm 0.01$  on Fahal ( $n = 96$ ). On average, 99.3% of nests with at least one egg went on to fledge at least one chick on Fahal and 83.7% on the Daymaniyats; the effect of island on brood size was significant ( $z = 3.076$ ,  $P = 0.002$ ). Random effects of year and nest-site were close to zero. Mean brood size differed among years, with brood size in 2013 being larger than in 2007 and 2010 only ( $P \leq 0.05$ ). Brood size showed an increasing trend over time ( $\beta = 0.04$ ,  $P = 0.044$ ). The number of chicks produced per productive nest (excluding failed nests;  $n = 196$ ) was  $2.43 \pm 0.057$ .

### Population dynamics

Estimates of demographic parameters revealed that survival of juvenile (i.e. pre-reproductive) birds was lower than that of the adults, and that breeding probability increased with age (Table 1). The overall asymptotic annual population growth rate ( $\lambda$ ) was 0.872 (95% CI 0.754–0.989), indicating a declining population. The cohort generation time was 5.9 years and the life expectancy at hatching was 2.5 years. Elasticity analysis indicated that  $\lambda$  was proportionately most sensitive to changes in adult, followed by juvenile, survival rate; the

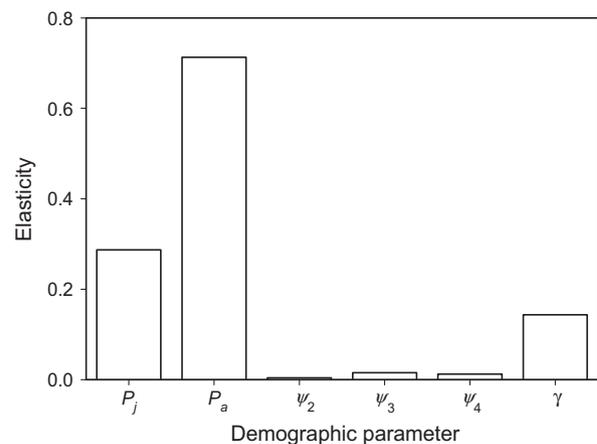
proportional influence of age-specific breeding probabilities on  $\lambda$  was insubstantial (Fig. 4).

Using island group-specific estimates of productivity,  $\lambda$  was slightly higher in Fahal than in the Daymaniyat Islands (Fahal:  $\lambda = 0.891$ , 95% CI 0.772–1.011; Daymaniyats:  $\lambda = 0.856$ , 95% CI 0.738–0.974). To evaluate the level of dispersal needed for  $\lambda$  to be around 1.0 (i.e. stable population) we calculated  $\lambda$  for a range of dispersal rates, assuming that dispersal occurs in the first or second year of life. Results indicated that  $\lambda$  approached 1.0 for a dispersal rate of about 35% (Fig. 5), which leads to a true juvenile survival rate of 0.88, higher than the adult survival rate. Our results indicate that the population of Sooty Falcons nesting in Oman may be declining at a rate of 5% (assuming a dispersal rate of 25%) to 10% (assuming a dispersal rate of 10%) annually.

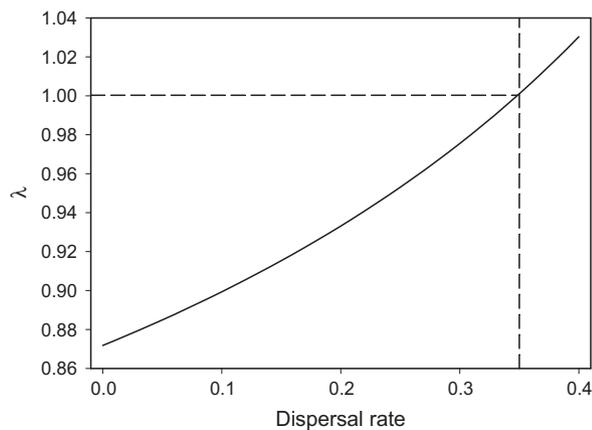
### DISCUSSION

Estimates of reproductive parameters and population growth rates suggest that Sooty Falcons in Oman are declining. These findings are consistent with conclusions of McGrady *et al.* (2016) based solely on survival information, and raise substantial concerns regarding the conservation status of Sooty Falcons, as Oman has been seen as a breeding stronghold.

Mean values for Sooty Falcon clutch and brood sizes were similar to those from elsewhere, most of which are not recent and have small sample



**Figure 4.** Elasticity of population growth rate to changes in vital demographic parameters.  $P_j$ ,  $P_a$  = survival of juveniles and adults;  $\psi_i$  = breeding probability of age class  $i$ ;  $\gamma$  = productivity (number of chicks produced by a breeding pair).



**Figure 5.** The relationship between dispersal rate and finite population growth rate ( $\lambda$ ) in Sooty Falcons nesting in Oman. Note that true survival rate = apparent survival rate/(1 – dispersal rate). The value of dispersal rate needed to yield a stable population ( $\lambda = 1.0$ ) is indicated by the vertical broken line.

sizes (Table 2). Our estimate for mean clutch size may have been somewhat underestimated because we could not account for eggs that disappeared before we visited nests in August. Because of the timing of our fieldwork, a smaller possibility was that we recorded incomplete clutches. We saw no evidence of nest predation or disturbance during the egg stage, although humans robbed eggs in 1978 (H. Walter pers. comm.). The inaccessibility

of some nests, especially on Fahal, may have protected them from human disturbance. There are no ground predators on any of the islands, and nests are usually in locations that make predation by avian predators (e.g. gulls) difficult.

In this study, 11.7% of active nests were unproductive. The observed value for brood size is likely to be lower than the actual value due to undocumented early nestling stage mortality. Human activities may have affected brood size on the Daymaniyats; we had strong evidence that one brood was taken, and signs of campfires were found in areas where Sooty Falcons might breed (and did so in 1978; Walter 1979b). We saw no evidence of human disturbance on Fahal Island during the nestling period. Although Fahal is nearer to shore and the populated capital area, landing is difficult, and policing is easier and likely to be more effective than on the Daymaniyat Islands.

About two-thirds of eggs produced chicks to ringing age, which was lower than that reported by Gaucher *et al.* (1994) (87.4%, CI 76.6–96.8) in Saudi Arabia. Furthermore, a difference in apparent hatching rate between our study and that in Saudi Arabia persisted even when we excluded the year in which hatching success rate was lowest (2007) to remove the potential effect of an early breeding period pulse of plentiful food (i.e. locusts Orthoptera, see below). We did not collect data

**Table 2.** Published estimates of Sooty Falcon clutch and brood sizes ( $\pm$  se, if reported).

Country	Locale	Years of study	Mean clutch size	Mean brood size	Reference
Oman	Daymaniyat Islands	8	2.92 $\pm$ 0.08; $n = 100$	1.85 $\pm$ 0.11; $n = 130$	This study
	Fahal Island	8	2.66 $\pm$ 0.08; $n = 53$	2.46 $\pm$ 0.11; $n = 96$	This study
Oman	Daymaniyat Islands	1	2.86 $\pm$ 0.10; $n = 21$	2.54 $\pm$ 0.29; $n = 13$	Walter (1979b)
	Fahal Island	1	2.31 $\pm$ 0.17; $n = 13$	2.0 $\pm$ 0.30; $n = 12$	Walter (1979b)
Bahrain	Hawar Islands	8		1.21; $n = 88$	Kavanaugh & King (2008)
Eritrea	Dahlac Archipelago	1	2.4 $\pm$ 0.51; $n = 5$	2.4 $\pm$ 0.17; $n = 6$	Clapham (1964)
Libya	Near Calanscio Serir	1	3.0 $\pm$ 0.0; $n = 1$		Booth (1961)
Saudi Arabia	'small Red Sea island'	1	2.33 $\pm$ 0.33; $n = 3$	2.00 $\pm$ 1.00; $n = 2$	Gaucher (1988)
Saudi Arabia	'Three islets north of Al Lith'	3	2.34; $n = 81$	2.05; $n = 81$	Gaucher <i>et al.</i> (1994)
Saudi Arabia	Farasan Islands	1		1.14 $\pm$ 0.33*; $n = 14$	Gaucher <i>et al.</i> (1995)
Saudi Arabia	Qishran	1		2.30 $\pm$ 0.21*; $n = 20$	Gaucher <i>et al.</i> (1995)
Israel	Negev Desert	12	2.78 $\pm$ 0.15; $n = 9$	2.0 $\pm$ 0.15; $n = 24$	Frumkin & Pinshow (1983), Frumkin (1988)
Israel	Tiran Island	1	3.0 $\pm$ 1.00; $n = 2$	3.0 $\pm$ 1.00; $n = 2$	Frumkin & Pinshow (1983), Frumkin (1988)
UAE	Abu Dhabi	1	2.8 $\pm$ 0.18; $n = 5$	2.8 $\pm$ 0.18; $n = 5$	Shah <i>et al.</i> (2008)

\*Chicks/territorial pair.

that would allow us to determine mean laying date, but breeding in 2007 did not seem to us to be earlier than in other years.

Nesting, hatching success rates and productivity may be influenced by food availability (Newton 1979, Dawson & Bortolotti 2000, Hoy *et al.* 2016). In the case of Sooty Falcons (and Eleonora's Falcons), food stress when nestlings are young is mitigated by the nestling period coinciding with increased food supply during autumn bird migration (Newton 1979, Walter 1979b), but it is not clear how they deal with pre-breeding and laying-time food shortages. Numerous locust remains indicated that they were abundant and eaten by Sooty Falcons during pre-breeding in 2007, when average clutch size was at its greatest ( $3.04 \pm 0.032$ ), although complete nest failures during hatching were also at their highest (26.7%), and the percentage of eggs that hatched at its lowest (37.7%). This pattern suggests to us that Sooty Falcons fed well on locusts in July to very early August 2007 and laid large clutches, but many nests failed completely sometime later because food availability levels were not maintained. Egg stage fieldwork in 2007, the year in which locusts may have boosted clutch size, was carried out only on the Daymaniyats (Table S1), accounting for the non-significant difference between the island groups.

Food shortage during the pre-laying period could result in smaller clutches (Newton 1979). Sooty Falcons typically arrive in Oman in May (Eriksen & Victor 2013), when prey numbers in Oman are naturally low. For the better studied Eleonora's Falcon, which also encounters low abundance of prey during pre-breeding, Walter (1979a) states that it lays fewer eggs than almost any European falcon, and summary data (Cramp & Simmons 1980, del Hoyo *et al.* 1994) seem to support the suggestion that Eleonora's Falcons produce more single egg clutches and fewer large clutches than other falcons, although there is much overlap. Only six (3.9%) of the clutches we recorded contained a single egg.

If eggs hatched, nestlings appeared to survive well because by then the migration of prey had commenced and food was sufficient, ground predators were absent, nests were protected from the elements, and avian predation and human disturbance were generally low. Although mortality was apparently low between ringing and fledging at the few nests we observed, we did find runt nestlings,

fledged falcons that drowned and, in 2012, a Bonelli's Eagle *Aquila fasciata* preyed on just-fledged falcons on Fahal for a few days. Steen *et al.* (2016) recorded Eleonora's Falcon nestlings being predated by non-parent conspecifics, and this could have happened in our study. These observations indicate that mortality can occur just around fledging. From our study area, eight of 12 (67%) radiotagged juvenile birds apparently died on their first migration (McGrady & Gschweg 2011, McGrady 2014), and McGrady *et al.* (2016) estimated apparent survival to average age at first breeding (*c.* 3.8 years) to be 0.57.

Overall, the nesting success rate on Fahal Island was higher than on the Daymaniyat Islands, and was higher or equal to that on the Daymaniyats in each of the 6 years for which we had data. Although Fahal Island supports no avian prey for falcons, it is close to Muscat, and Sooty Falcons hunt above the city. The nearest onshore areas to the Daymaniyats are more distant than at Fahal, and probably have lower densities of potential prey during pre-breeding because there is less residential and municipal irrigation. Although some smaller sea birds that falcons prey upon (e.g. Bridled Tern *Onychoprion anaethus*, 95–150 g; White-cheeked Tern *Sterna repressa*, 113–142 g, del Hoyo *et al.* 1996) breed on the Daymaniyat Islands in June and July (Eriksen & Victor 2013, Al Fazari & Victor 2014), the impression was that falcon prey was not abundant there during early breeding. Xirouchakis *et al.* (2012) found a negative relationship between Eleonora's Falcon nesting success and distance to the mainland. We suggest that the higher nesting success rate and productivity observed on Fahal is largely the result of falcons being able to forage on the mainland, where food supply is relatively high, especially when prey birds are not migrating.

Other factors may also contribute to the differences in reproduction between the island groups, including nesting density. Fahal covers 0.127 km<sup>2</sup> and supports one of the highest nesting densities of Sooty Falcons in the world (Gallo Orsi *et al.* 2014). The Daymaniyat Islands are a chain of nine islands, ranging in size from 0.01 to 0.46 km<sup>2</sup> and separated by 0.1–9.0 km, that stretch over about 21 km (Fig. 1). Some of the Daymaniyat Islands support no breeding falcons (D1, D8), some single breeding pairs (D2, D3 in all but 1 year, D6), others with pairs separated by hundreds of metres (D4, D5, D7), and some where pairs are separated

by tens of metres (D9, D3 in 2007). It is not inconceivable that differences in population density may explain some of the island-specific differences. Colony size in Lesser Kestrel *Falco naumanni* affects both dispersal (dispersal from small colonies to large ones more likely, and dispersal between colonies negatively related to distance) and survival (survival of adults is higher in larger colonies) (Serrano & Tella 2003, Serrano *et al.* 2005). However, potentially important differences between Lesser Kestrel and the Sooty Falcons exist (e.g. diet, existence of ground predators), suggesting caution when making comparisons. More work is needed to investigate the costs and benefits resulting from coloniality in Sooty Falcons.

Demographic analyses are crucial for determining population status, diagnosing causes of past declines, identifying management targets and developing plans for the conservation of wildlife species (e.g. Caswell 2001). Our analyses of matrix population models parameterized with the vital rates estimated for our study population (this study, McGrady *et al.* 2016) suggested that the finite annual population growth rate  $\lambda$  was substantially lower than 1.0, for the overall population or for the Daymaniyats individually, because point estimates of  $\lambda$  were  $<0.9$  and confidence intervals did not overlap 1.0. For Fahal Island, however, confidence intervals for  $\lambda$  overlapped 1.0, although the point estimate was quite low, which would indicate a declining population. Taken together, our results provide evidence that our study population in Oman was declining. Nonetheless, we note that our model was based on estimates of apparent survival rather than true survival. Because estimates of apparent survival from capture-mark-recapture analyses include losses from both death and dispersal, estimates of apparent survival are always lower than true survival for dispersing age classes. The true juvenile survival rate needed to maintain a stable population (0.88) is higher than the apparent survival for juvenile and adult Sooty Falcons reported by McGrady *et al.* (2016), and is at a level rarely observed in raptors, even for larger species (e.g. Smith *et al.* 2015, Newton *et al.* 2016).

Elasticity analyses suggested that the asymptotic population growth rate was proportionately most sensitive to changes in survival of adults, followed by that of juveniles. These results are consistent with elasticity patterns for other raptors (Hiraldo

*et al.* 1996), as well as a now well-established pattern that growth rates of populations characterized by delayed maturity tend to be proportionately the most sensitive to changes in survival rates, and relatively insensitive to reproductive parameters (Oli & Dobson 2003, Stahl & Oli 2006). Satellite radiotracking studies suggest that most juvenile Sooty Falcons die within months during their first migration (McGrady *et al.* 2016), and the life expectancy at hatching calculated by us (2.5 years) was well below the mean age of first breeding ( $3.76 \pm 1.48$ ) of falcons on these islands (McGrady *et al.* 2016). High mortality of adults and juveniles away from the breeding grounds may be the primary cause of the apparent population decline (Kavanaugh & King 2008, BirdLife International 2017).

Although the importance of adult and juvenile survival in driving population dynamics is well established and was also confirmed in our study, reproductive success is also an important determinant of fitness and population growth rate (Clutton-Brock 1988, Newton 1989, Oli & Dobson 2003, Stahl & Oli 2006). In the case of Sooty Falcons, productivity may assume greater importance in Oman because it is on the edge of its global breeding range and distant from other breeding strongholds (Red Sea breeding areas are  $>1800$  km away). Reliable estimates of natal dispersal are not available for Sooty Falcon (McGrady *et al.* 2016) or the ecologically similar Eleonora's Falcon (but see Wink *et al.* 1985, Ristow *et al.* 1989), but lower production in Oman could result in fewer recruits there. Still, given the results of our elasticity analysis, and what is known from other raptors (e.g. Real & Mañosa 1997, Prugnolle *et al.* 2003, Craig *et al.* 2004) Sooty Falcon conservation efforts should prioritize reducing adult mortality, which we suspect is concentrated away from the breeding areas.

Our estimate of population growth rate suggests the Oman population is in decline, and natural recovery may be difficult if the population becomes very small or disappears, especially if natal site fidelity is high and natural immigration low. Information on increasing raptor populations, especially reintroduced ones, shows that range expansion is sometimes slow or patchy (e.g. Evans *et al.* 1999, Schaub *et al.* 2009, Whitfield *et al.* 2009), although the species studied may have been affected by persecution or contaminants (e.g. Mora *et al.* 1997, Hunt *et al.* 2009). However,

other species, such as Peregrine Falcon *Falco peregrinus*, have recovered from past declines (Cade & Burnham 2003).

Although this study and McGrady *et al.* (2016) provided new, up-to-date information on the population ecology of Sooty Falcons in Oman, the lack of data from other parts of the breeding range and the wintering grounds made some analyses impossible (e.g. dispersal) (McGrady *et al.* 2016). This paucity of data may have contributed to the relatively low level of conservation concern in the past. Our results and those of others (Kavanaugh & King 2008, McGrady *et al.* 2016) highlight potential constraints (e.g. geographical isolation, mortality in non-breeding areas) in the species' western breeding range relevant to its conservation at all geographical scales. Sooty Falcons also nest singly, and the demographic drivers that affect that portion of the population may be different than in the colonial situation. Studies of solitary nesting Sooty Falcons are needed for the development of a comprehensive conservation strategy, and simultaneous studies of island aggregations and singly breeding populations could illuminate more general principles related to the costs and benefits of those two breeding strategies.

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, the Ministry of Environment and Climate Affairs (MECA) and Arid Lands. 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. 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, P. McGrady, M. Hurst, R. Eaton, A. Thorpe, N. Williams, M. Gschweng, L. Arison, G. Razafimanjato and M. Fisher. The help provided by Said Al-Sayabi of the Royal Yachts was vital to the success of the work. The work was performed in accordance with the laws of the Sultanate of Oman. We thank R. Kimball, S. Roos and two anonymous reviewers for many helpful comments.

## REFERENCES

- Agresti, A. 2015. *Foundations of Linear and Generalized Linear Models*. Hoboken, NJ: John Wiley & Sons.
- Al Fazari, W.A. & Victor, R. 2014. Observations on the nesting ecology of seabirds in Al-Daymaniat Islands. *Int. J. Ecol. Environ. Sci.* **40**: 219–224.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singman, H., Dai, B., Grothendieck, G. & Green, P. 2016. *Package lme4*. <https://github.com/lme4/lme4/> <http://lme4.r-forge.r-project.org/>
- BirdLife International 2017. Species factsheet: *Falco concolor*. <http://www.birdlife.org> (accessed 29 January 2017).
- Booth, B.D. 1961. Breeding of the Sooty Falcon in the Libyan desert. *Ibis* **103**: 129–130.
- Cade, T.J. & Burnham, W. 2003. *Return of the Peregrine: a North American saga of Tenacity and Teamwork*. Boise, ID: The Peregrine Fund Inc.
- Caswell, H. 2001. *Matrix Population Models: Construction, Analysis and Interpretation*. Sunderland, MA: Sinauer Associates.
- Clapham, C.S. 1964. The birds of the Dahlac archipelago. *Ibis* **106**: 376–388.
- Clutton-Brock, T.H. 1988. Reproductive success. In Clutton-Brock, T.H. (ed.) *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*: 472–485. Chicago: University of Chicago Press.
- Convention on Migratory Species 2008. *Species memorandum of understanding on the conservation of migratory birds of prey in Africa and Eurasia*. <http://www.cms.int/raptors/en/page/agreement-text> (accessed 27 April 2017).
- Craig, G.R., White, G.C. & Enderson, J.H. 2004. Survival, recruitment, and rate of population change of the Peregrine Falcon population in Colorado. *J. Wildl. Manage.* **68**: 1032–1038.
- Cramp, S. & Simmons, K.E.L. 1980. *Handbook of the Birds of Europe the Middle East and North Africa – Birds of the Western Palearctic, Vol. 2*. Oxford: Oxford University Press.
- Dawson, R.D. & Bortolotti, G.R. 2000. Reproductive success of American Kestrels: the role of prey abundance and weather. *Condor* **102**: 814–822.
- Eriksen, J. & Victor, R. 2013. *Oman Bird List*, 7th edn. Muscat: Center for Environmental Studies and Research.
- Evans, M.I. 1994. *Important Bird Areas in the Middle East*. Cambridge: BirdLife International.
- Evans, I.M., Summers, R.W., O'Toole, L., Orr-Ewing, D.C., Evans, R., Snell, N. & Smith, J. 1999. Evaluating the success of translocating Red Kites *Milvus milvus* to the UK. *Bird Study* **46**: 129–144.
- Frumkin, R. 1988. Biologie und Bestimmung des Schieferfalken *Falco concolor*. *Limicola* **2**: 83–109.
- Frumkin, R. & Pinshow, B. 1983. Notes on the breeding ecology and distribution of the Sooty Falcon *Falco concolor* in Israel. *Ibis* **125**: 251–259.
- Gallo Orsi, U., Williams, N.P., Javed, S. & McGrady, M. 2014. *Draft International Single Species Action Plan for the Sooty Falcon Falco concolor*. Abu Dhabi, UAE: Convention on Migratory Species.
- Gaucher, 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., Daunicht, W.D. & Eichacher, X. 1994. The Sooty Falcon *Falco concolor* in Saudi Arabia. In Meyburg, B.-U. & Chancellor, R.D. (eds) *Raptor Conservation Today*:

- 109–116. London: World Working Group on Birds of Prey and Owls and Pica Press.
- 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.
- Hiraldo, F., Negro, J.J., Donazar, J.A. & Gaona, P.** 1996. A demographic model for a population of the endangered Lesser Kestrel in southern Spain. *J. Appl. Ecol.* **33**: 1085–1093.
- Hoy, S.R., Millon, A., Petty, S.J., Whitfield, D.P. & Lambin, X.** 2016. Food availability and predation risk, rather than intrinsic attributes, are the main factors shaping the reproductive decisions of a long-lived predator. *J. Anim. Ecol.* **85**: 892–902.
- del Hoyo, J., Elliott, A. & Sargatal, J.** 1994. *The Handbook of Birds of the World, Vol. 2*. Barcelona: Lynx Edicions.
- del Hoyo, J., Elliott, A. & Sargatal, J.** 1996. *The Handbook of Birds of the World, Vol. 3*. Barcelona: Lynx Edicions.
- Hunt, W.G., Parish, C.N., Orr, K. & Aguilar, R.F.** 2009. Lead poisoning and the reintroduction of the California Condor in northern Arizona. *J. Avian. Med. Surg.* **23**: 145–150.
- Kavanaugh, 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.
- Klaassen, R.H., Hake, M., Strandberg, R., Koks, B.J., 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.
- Lebreton, J.D., Hines, J.E., Pradel, R., Nichols, J.D. & Spendelov, J.A.** 2003. Estimation by capture-recapture of recruitment and dispersal over several sites. *Oikos* **101**: 253–264.
- Manlik, O., McDonald, J.A., Mann, J., Raudino, H.C., Bejder, L., Krüchten, M., Conner, R.C., Heithaus, M.R., Lacy, R.C. & Sherwin, W.B.** 2016. The relative importance of reproduction and survival for the conservation of two dolphin populations. *Ecol. Evol.* **6**: 3496–3512.
- McGrady, M.J.** 2014. <http://sootyfalcon.blogspot.co.at/> (accessed 16 February 2017).
- McGrady, M.J. & Gschweng, M.** 2011. <http://sootyfalconoman.blogspot.co.at/> (accessed 16 February 2017).
- McGrady, M.J., Al Fazari, W., Al Jahdhami, M.H. & Oli, M.K.** 2016. Survival of Sooty Falcons (*Falco concolor*) in Oman. *J. Ornithol.* **157**: 427–437.
- Mora, M.A., Lee, M.C., Jenny, J.P., Schultz, T.W., Sericano, J.L. & Clum, N.J.** 1997. Potential effects of environmental contaminants on recovery of the Aplomado Falcon in south Texas. *J. Wildl. Manage.* **61**: 1288–1296.
- Newton, I.** 1979. *Population Ecology of Raptors*. Berkhamstead: T. & A.D. Poyser.
- Newton, I. (ed.)** 1989. *Lifetime Reproduction in Birds*. London: Academic Press.
- Newton, I.** 1998. *Population Limitation in Birds*. London: Academic Press.
- Newton, I., McGrady, M.J. & Oli, M.K.** 2016. A review of survival estimates from raptors and owls. *Ibis* **158**: 227–248.
- Oli, M.K. & Dobson, F.S.** 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *Am. Nat.* **161**: 422–440.
- 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.
- QGIS** 2014. *QGIS desktop 2.6*. <http://www.qgis.org/en/site/> (accessed 16 February 2017).
- R Core Team** 2014. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org/>
- Real, J. & Mañosa, S.** 1997. Demography and conservation of western European Bonelli's Eagle *Hieraetus fasciatus* populations. *Biol. Conserv.* **79**: 59–66.
- Ristow, D., Scharlau, W. & Wink, M.** 1989. Population structure and mortality of Eleonora's falcon *Falco eleonora*. In Meyburg, B.-U. & Chancellor, R.D. (eds) *Raptors in the Modern World*: 321–326. London: World Working Group on Birds of Prey and Owls.
- Sæther, B.E. & Bakke, Ø.** 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**: 642–653.
- Schaub, M., Zink, R., Beissmann, H., Sarrazin, F. & Arlettaz, R.** 2009. When to end releases in reintroduction programmes: demographic rates and population viability analysis of Bearded Vultures in the Alps. *J. Appl. Ecol.* **46**: 92–100.
- Semere, D., Hagos, T., Seleba, G., Gebrezgabhier, Y., Haile, Z., Chiozzi, G. & De Marchi, G.** 2008. The status of breeding seabirds and waterbirds on the Eritrean Red Sea islands. *Bull. Afr. Bird Club* **15**: 228–237.
- Serrano, D. & Tella, J.L.** 2003. Dispersal within a spatially structured population of Lesser Kestrels: the role of spatial isolation and conspecific attraction. *J. Anim. Ecol.* **72**: 400–410.
- Serrano, D., Oro, D., Ursúa, E. & Tella, J.L.** 2005. Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. *Am. Nat.* **166**: E22–E31.
- Shah, J.N., Khan, S.B., Ahmed, S., Javed, S. & Hammadi, A.** 2008. Sooty Falcon in the United Arab Emirates. *Falco* **32**: 16–19.
- Smith, G.D., Murillo-García, O.E., Hostetler, J.A., Mearns, R., Rollie, C., Newton, I., McGrady, M.J. & Oli, M.K.** 2015. Demography of population recovery: survival and fidelity of Peregrine Falcons at various stages of population recovery. *Oecologia* **178**: 391–401.
- Stahl, J.T. & Oli, M.K.** 2006. Relative importance of avian life-history variables to population growth rate. *Ecol. Model.* **198**: 23–39.
- Steen, R., Milou, A., Tsimpidis, T., Selås, V. & Sonerud, G.A.** 2016. Nonparental infanticide in colonial Eleonora's Falcons (*Falco eleonora*). *J. Raptor Res.* **50**: 217–220.
- Steenhof, K. & Newton, I.** 2007. Assessing nesting success and productivity. In Bird, D.M. & Bildstein, K.L. (eds) *Raptor Research and Management Techniques*: 181–192. Surrey: Hancock House.
- Walter, H.** 1979a. *Eleonora's Falcon. Adaptions to Prey and Habitat in a Social Raptor*. Chicago: University of Chicago Press.
- Walter, H.** 1979b. The Sooty Falcon (*Falco concolor*) in Oman: results of a breeding survey, 1978. *J. Oman Stud.* **5**: 9–60.

- Whitfield, D.P., Douse, A., Evans, R.J., Grant, J., Love, J., McLeod, D.R., Reid, R. & Wilson, J.D.** 2009. Natal and breeding dispersal in a reintroduced population of White-tailed Eagles *Haliaeetus albicilla*. *Bird Study* **56**: 177–186.
- Williams, B.K., Nichols, J.D. & Conroy, M.J.** 2001. *Analysis and Management of Animal Populations*. San Diego: Academic Press.
- Wink, M., Ristow, D. & Wink, C.** 1985. Biology of Eleonora's Falcon (*Falco eleonora*): 7. variability of clutch size, egg dimensions and egg coloring. *J. Raptor Res.* **19**: 8–15.
- Xirouchakis, S.M., Fric, J., Kassara, C., Portolou, D., Dimalexis, A., Karris, G., Barboutis, C., Latsoudis, P., Bourdakis, S., Kakalis, E. & Sfenthourakis, S.** 2012. Variation in breeding parameters of Eleonora's Falcon (*Falco eleonora*) and factors affecting its reproductive performance. *Ecol. Res.* **27**: 407–416.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M.** 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer.

Received 29 September 2016;  
revision accepted 29 May 2017.  
Associate Editor: Staffan Roos.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Timing of Sooty Falcon fieldwork during 2007–2014.

**Table S2.** Numbers of nesting territories per island on Fahal and the Daymaniyat Islands (D1–D9), Oman, during 2007–2014 that contributed data to our analyses.