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

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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 (±SE) clutch and brood size was 2.83 ±0.06 and 2.11 ±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 ±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 (λ) was 0.87 (95% CI: 0.75 - 0.99), suggesting a declining population, though Sooty Falcons on Fahal enjoyed a slightly higher population growth rate than on the Daymaniyats. Because our study population is on the edge of the breeding range and 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: Sooty Falcon; Oman; reproduction; population growth; breeding success; hatching rate

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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 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 eleonorae*. 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 1994; Gaucher *et al.* 1995; Kavanaugh & King 2008, Appendix 1). 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 1979; Gaucher *et al.* 1995; McGrady and Office for the Conservation of the Environment, unpublished 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.* 2012). 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 modeling of the population is an important step to filling knowledge gaps.

Using data from a seven-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 in order 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 characteristic 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 north eastern 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 1994; BirdLife International 2017).

Significant numbers of Sooty Falcons may breed on mainland sites, though 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 comprise 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 (Kavenaugh & King 2008), which are about 800 km distant; a few pairs breed in 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^o N, 58.50^o E), and the nine islands in the Daymaniyat archipelago (23.85^o N, 58.09^o E, D1 (farthest east) to D9 (farthest west)). Oman's breeding population is almost entirely found on these islands (Walter 1979b; Office of Conservation of the Environment & M. McGrady, unpublished 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 only 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 Supplementary Online Table S2.

In most years, two bouts of field work 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 (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. Field work 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 1-4 observers using binoculars and a boatman in 3- to 8-m motorboats; searches on foot were made by 1-6 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 land or sea. At accessible nests we determined whether they were 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 ± 1 standard error 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 (GLMM; 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 difference 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 2016). Maps were produced using QGIS desktop (ver. 2.6, 2014).

Demographic analysis

We constructed and analyzed 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:

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

where F_i is age-specific fertility rate calculated using the post-breeding census method, and

assuming 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 γ is the average number of chicks produced by a breeding pair per year and ψ_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 again encountered

until they return as breeders; only about 4% of falcons ringed as hatchling 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 γ as the number of chicks hatched per nest per year, considering only nests with complete chick counts. P_j, P_a and ψ_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 (λ), stable stage distribution, reproductive values, age-specific life-expectancy and the proportional sensitivity (elasticity) of λ to lower-level vital rates. The delta method was used to estimate variance and confidence intervals of λ (Caswell 2001). Variances of P_j, P_a and ψ_i were estimated using multistate capture-mark-recapture models, and that of γ 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 λ. Because we did not have data-based estimates of natal dispersal rates, we assumed that dispersal predominantly occurs during the first year of life, and calculated λ for a range of natal dispersal rates.

RESULTS

Productivity

Overall, clutches comprised a mean of 2.83 ± 0.06 eggs per nest (n=153, range:1-4); 83 were three-egg clutches. Mean clutch size was 2.92 ± 0.08 on the Daymaniyats (n=100), and 2.66 ± 0.08 on Fahal (n=53). Annual mean egg production on the Daymaniyats varied between 2.40 (2009) and

3.27 (2014), 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), nor was there evidence for temporal trend (β = 0.013 ± 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 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; random effect of nest location was practically zero. There was no evidence for year-to-year difference in nesting success (P > 0.05). There was an increasing trend in nesting success over time (β = 0.298 ± 0.100, P = 0.003).

On average, 66.4 ± 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 was significant (P < 0.05), with hatching success in 2007 being lower than in all other years, except 2014. However, there was no evidence of temporal trend in hatching success (β = 0.118 ± 0.082, P = 0.152).

Mean brood size was 2.11 ± 0.074 per active nest (nests ≥ one egg, n = 226); it ranged from 1.76 ± 0.031 in 2010 to 2.65 ± 0.0325 in 2013. The mean on the Daymaniyats was 1.85 ± 0.01 (n = 130) and 2.45 ± 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; 83.7% for 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 ≤0.05). Brood size showed an increasing trend over time (β = 0.04, P = 0.044).The number of chicks produced per productive nest (excluding failed nests; n = 196) was 2.43 ± 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 (λ) was 0.872 (95% CI: 0.754 – 0.989), indicating a declining population. The cohort generation time was 5.9 yrs, and the life expectancy at hatching was 2.5 yrs. Elasticity analysis indicated that λ was proportionately most sensitive to changes in adult, followed by juvenile, survival rate; the proportional influence of age-specific breeding probabilities on λ was insubstantial (Fig. 4).

Using island group-specific estimates of productivity, λ was slightly higher in Fahal than in Daymaniyat Islands (Fahal: λ = 0.891; 95% CI: 0.772 – 1.011; Daymaniyats: λ = 0.856; 95% CI: 0.738 – 0.974). To evaluate the level of dispersal needed for λ to be around 1.0 (i.e., stable population) we calculated λ for a range of dispersal rates, assuming that dispersal occurs in the first or second year of life. Results indicated that λ approached 1.0 for a dispersal rate of about 35% (Fig. 5), which leads to a true juvenile survival rate of 0.88, which is higher than adult survival rate. Taken together, our results indicate that the population of Sooty Falcons nesting in Oman may be declining at a rate of 5% (assuming dispersal rate of 25%) to 10% (assuming 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 because 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 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 field work, a lesser possibility was that we recorded incomplete clutches. We saw no evidence of nest predation or disturbance during the egg stage, though 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 actual 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 that would allow us to determine mean laying date, but breeding in 2007 did not seem to us to be earlier than 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 ± 0.032), though complete nest failures during hatching were also at their highest (26.7%), and the percentage of eggs that hatched was at its lowest (37.7%). This pattern suggests to us that Sooty Falcons fed well on locusts in July-very early August 2007 and laid large clutches, but many nests failed completely sometime later because food availability levels were not maintained. Egg stage field work 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, though 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 8 of 12 (67%) radio-tagged juvenile birds apparently died on their first migration (McGrady & Gschweng 2011; McGrady 2014), and McGrady *et al.* (2016) estimated apparent survival to average age at first breeding (c. 3.8 yrs) 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 six 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 residential and municipal irrigation is less. Although some smaller sea birds that falcons prey upon (e.g. Bridled Tern *Onychoprion anaetheus*, 95-150g; White-cheeked Tern *Sterna repressa*, 113-142g (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^2, 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 9 islands, ranging in size (0.01 km^2 – 0.46 km^2) 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 but1 year, D6), others with pairs separated by hundreds of meters (D4, D5. D7), and some where pairs are separated by tens of meters (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 is needed 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 for 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 λ was substantially lower than 1.0, for the overall population or for the Daymaniyats individually, because point estimates of λ were <0.9 and confidence intervals did not overlap 1.0. For Fahal Islands, however, confidence intervals for λ 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 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 adult, 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 most sensitive to changes in survival rates, and relatively insensitive to reproductive parameters (Oli & Dobson 2003; Stahl & Oli 2006). Satellite radio-tracking 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 yrs) was well below the mean age of first breeding (3.76 ± 1.48) of falcons on these islands (McGrady *et al.* 2016). High mortality of adult 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 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). While 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), 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 it becomes very small or disappears, especially if natal site fidelity is high and natural immigration low. Information on increasing raptor populations, especially reintroduced ones, show 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, like Peregrine Falcon *Falco peregrinus*, have recovered from past declines (Cade & Burnham 2003).

While this study and McGrady *et al.* (2016) have provided new, up-to-date information on 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 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.

LITERATURE CITED

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Table 1. Estimates of demographic parameters (mean ± SD) used to parameterize matrix population

model. Demographic P_j, P_a = survival of juveniles and adults; ψ_i = breeding probability of age class *i*,

and γ = productivity (number of chicks produced per breeding pair). Survival and breeding

probabilities were estimated by McGrady *et al*. (2016).

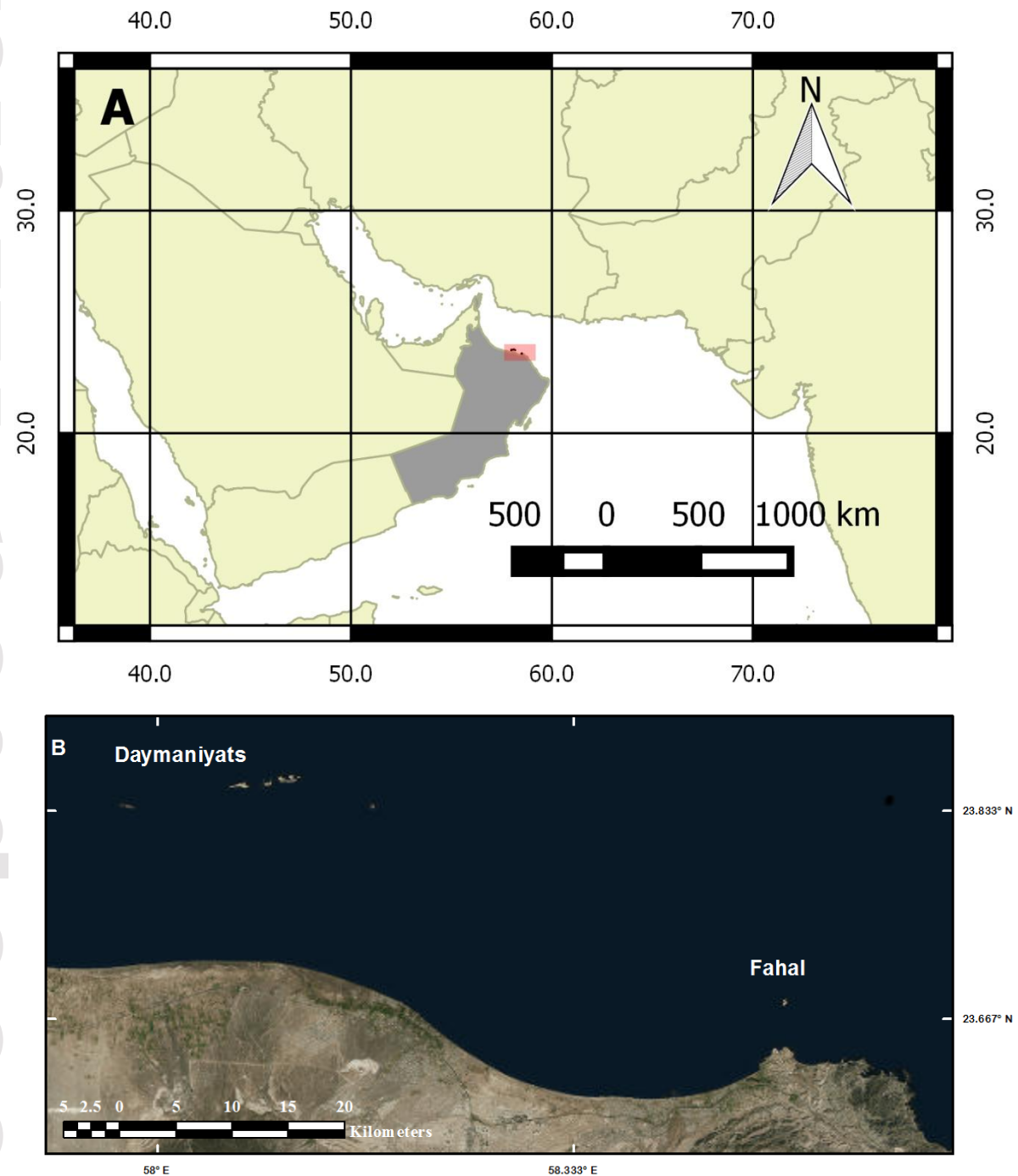| Parameter	Estimate
P_j	0.570 ± 0.048
P_a	0.656 ± 0.069
ψ_2	0.065 ± 0.036
ψ_3	0.159 ± 0.069
ψ_4	0.339 ± 0.211
γ	2.110 ± 0.048

Table 2. Published estimates of Sooty Falcon clutch and brood sizes (±SE, if reported).

Country	Locale	Years of study	Mean clutch size	Mean brood size	Reference
Oman	Daymaniyat Islands	8	2.92 ± 0.08; n = 100	1.85 ± 0.11; n=130	This study
	Fahal Island	8	2.66 ± 0.08; n=53	2.46 ± 0.11; n=96	This study
Oman	Daymaniyat Islands	1	2.86 ± 0.10; n=21	2.54 ± 0.29; n=13	Walter 1979b
	Fahal Island	1	2.31 ± 0.17; n=13	2.0 ± 0.30; n=12	Walter 1979b
Bahrain	Hawar Islands	8		1.21; n=88	Kavanaugh & King 2008
Eritrea	Dahlac Archipelago	1	2.4 ± 0.51; n=5	2.4 ± 0.17; n=6	Clapham 1964
Libya	Near Calanscio Serir	1	3.0 ± 0.0; n=1		Booth 1961
Saudi Arabia	"small Red Sea island"	1	2.33 ± 0.33; n=3	2.00 ± 1.00; n=2	Gaucher 1988

Country	Location		Productivity 1	Productivity 2	Reference
Saudi Arabia	"Three islets north of Al Lith"	3	2.34; n=81	2.05; n=81	Gaucher *et al.* 1994
Saudi Arabia	Farasan Islands	1		1.14 ± 0.33*; n=14	Gaucher *et al.* 1995
Saudi Arabia	Qishran	1		2.30 ± 0.21*; n=20	Gaucher *et al.* 1995
Israel	Negev Desert	12	2.78 ± 0.15; n=9	2.0 ± 0.15; n=24	Frumkin & Pinshow 1983; Frumkin 1988
Israel	Tiran Island	1	3.0 ± 1.00; n=2	3.0 ± 1.00; n=2	Frumkin & Pinshow 1983; Frumkin 1988
UAE	Abu Dhabi	1	2.8 ± 0.18; n=5	2.8 ± 0.18; n=5	Shah *et al.* 2008

*chicks/territorial pair

Figure 1. Map of the study area. A: regional scale, with Oman shaded (study area highlighted rectangle); B: islands comprising the study area; C: Daymaniyat Islands, which are about 15 km offshore; D: Fahal Island, which is about 4 km offshore.
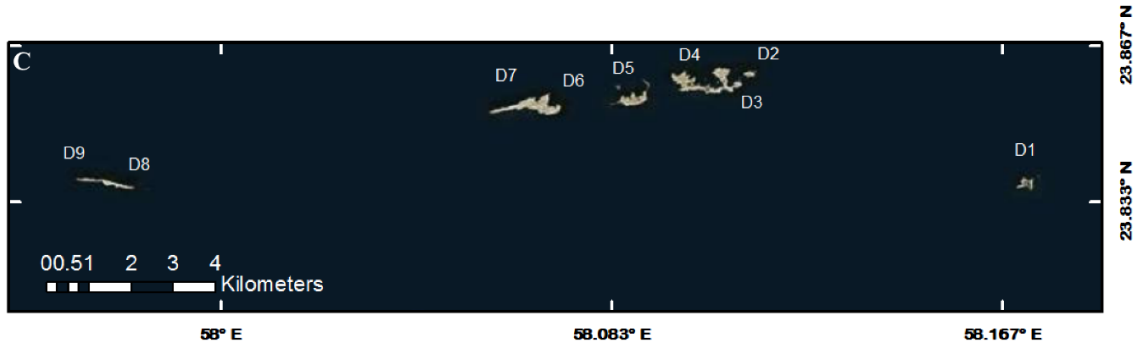
C

D9 D8

D7 D6 D5 D4 D2
                    D3

D1

23.867° N

23.833° N

00.51 2 3 4
Kilometers

58° E   58.083° E   58.167° E

D

0 50 100   200   300   400
                        Meters

23.683° N

23.681° N

23.678° N

58.497° E   58.5° E   58.503° E

Figure 2. The average (± 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.
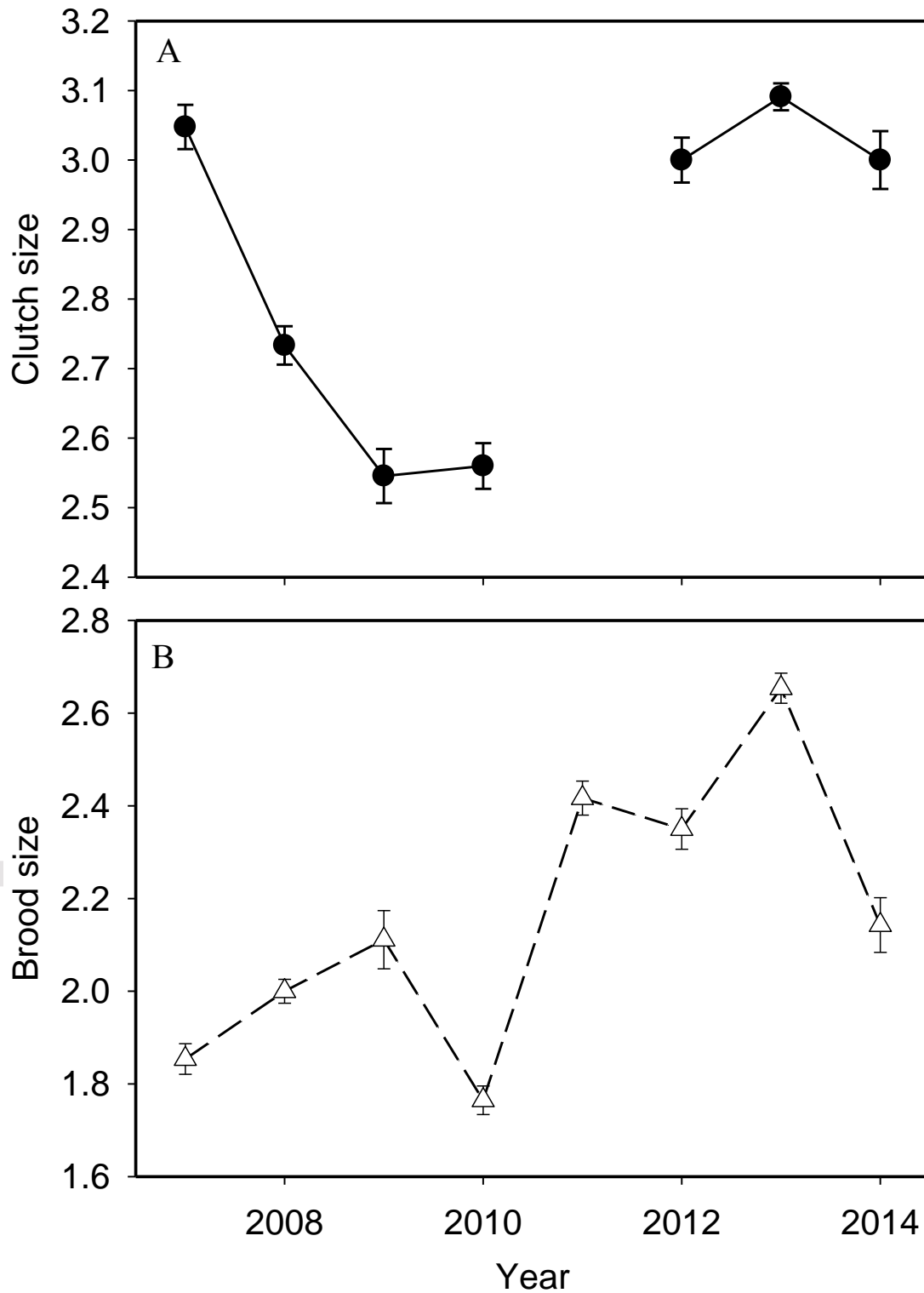
Figure 3. The average (± 1 SE) clutch and brood size for Sooty Falcons nesting on Fahal and the
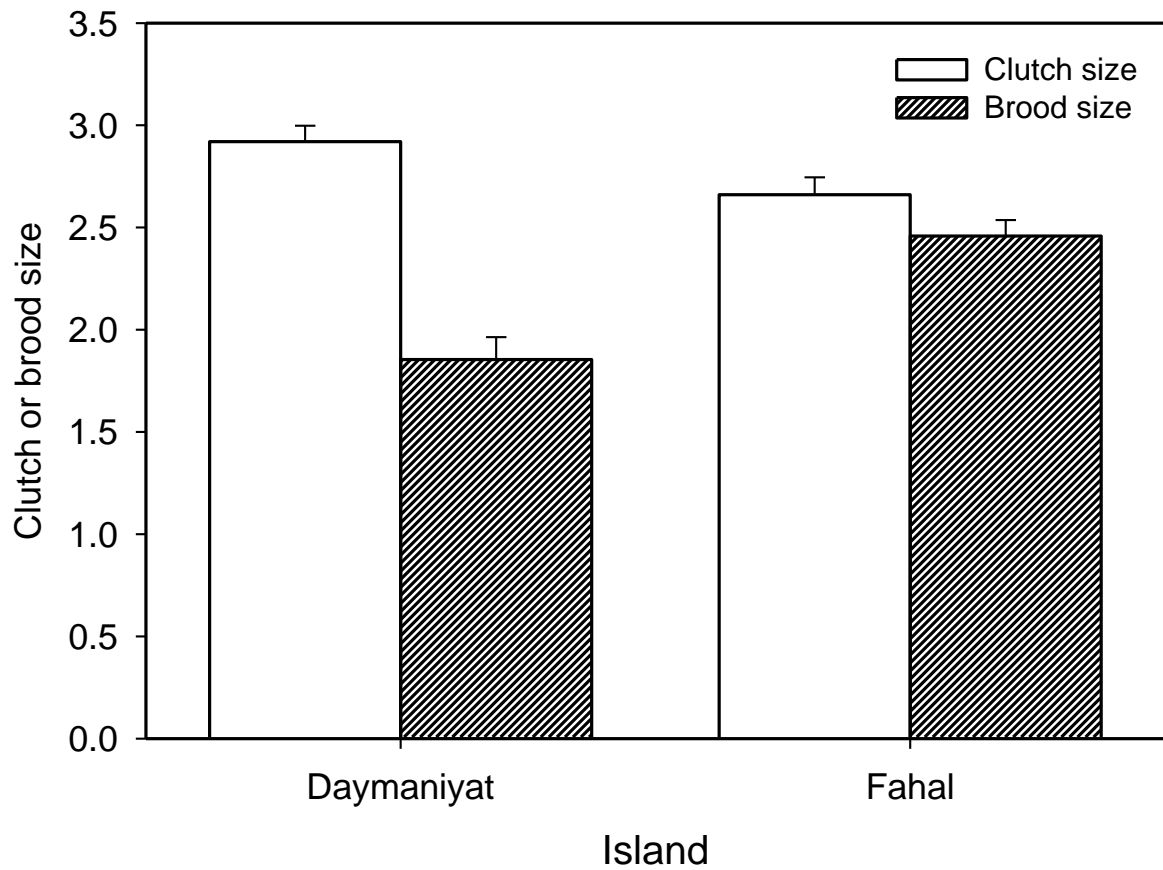
Daymaniyat Islands in Oman.

Figure 4. Elasticity of population growth rate to changes in vital demographic parameters. Symbols are: P_j, P_a = survival of juveniles and adults; ψ_i = breeding probability of age class i, and γ = productivity (number of chicks produced by a breeding pair).
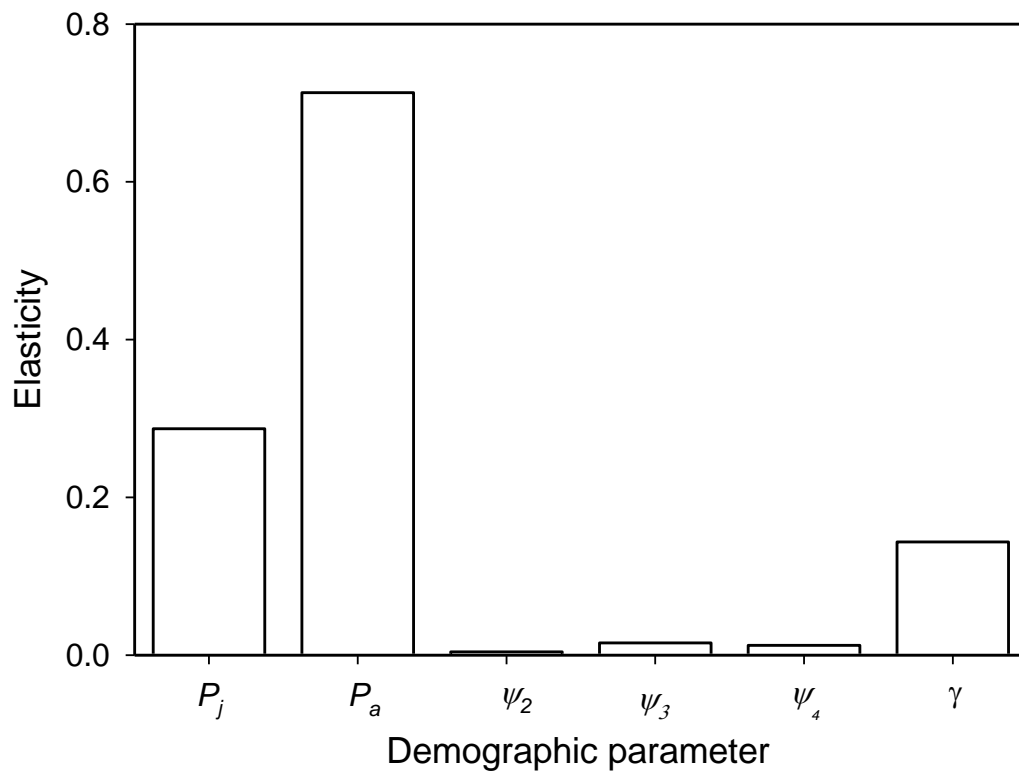
Figure 5. The relationship between dispersal rate and finite population growth rate (λ) in Sooty Falcons nesting in Oman. Note that true survival rate = apparent survival rate/(1-dispersal rate). The value of dispersal rate needed to yield a stable population (λ = 1.0) is indicated by the vertical broken line.