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Demographic consequences of nestbox use for Red-footed Falcons *Falco vespertinus* in Central Asia

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Nestbox programmes are frequently implemented for the conservation of cavity-nesting birds, but their effectiveness is rarely evaluated in comparison with birds not using nestboxes. In the European Palaearctic, Red-footed Falcon *Falco vespertinus* populations are both of high conservation concern and are strongly associated with nestbox programmes in heavily managed landscapes. We used a 21-year monitoring dataset collected on 753 nesting attempts by Red-footed Falcons in unmanaged natural or semi-natural habitats to provide basic information on this poorly known species; to evaluate long-term demographic trends within this population; and to evaluate response of demographic parameters of Red-footed Falcons to environmental factors including use of nestboxes. We observed significant differences among years in laying date, offspring loss and numbers of fledglings produced, but not in egg production. Of these four parameters, offspring loss and, to a lesser extent, number of fledglings exhibited directional trends over time. Variation in laying date and in numbers of eggs were not well explained by any one model of environmental factors, but instead by combinations of models, each with informative terms for nest type. Nevertheless, laying in nestboxes occurred 2.10 ± 0.70 days earlier than in natural nests. In contrast, variation in both offspring loss and numbers of fledglings produced were fairly well explained by a single model including terms for nest type, nest location and an interaction between the two parameters (65 and 81% model weights, respectively), with highest offspring loss in nestboxes on forest edges. Because, for other species, earlier laying dates are associated with more fit individuals, this interaction highlighted a possible ecological trap, whereby birds using nestboxes on forest edges lay eggs earlier but suffer greater offspring loss and produce lower numbers of fledglings than do those in other nesting settings. If nestboxes increase offspring loss for Red-footed Falcons in heavily managed landscapes where populations are at greater risk, or for the many other species of rare or endangered birds supported by nestbox programmes, these processes could have important demographic and conservation consequences.

Keywords: citizen science, Kazakhstan, long-term monitoring, nestbox programmes, unintended consequences.

Large sums of money are spent each year in support of species-specific biodiversity conservation programmes (McCarthy *et al.* 2012, Juffe-Bignoli *et al.* 2016). These programmes are generally based on information derived from research and expert opinion. Although best practice guidelines often recommend empirical evaluations of conservation actions, financial limitations or data constraints associated with small populations mean that such evaluations are uncommon (Maron *et al.* 2013, Evans *et al.* 2015). However, it seems clear

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that rigorous design and evaluation are likely to maximize the cost-effectiveness and biological relevance of conservation programmes (Evans *et al.* 2015).

One of the most common conservation actions implemented for birds is establishment of nestbox programmes and in heavily transformed landscapes, nestboxes may be the only option for enhancing population size (Negro *et al.* 2007). Nestboxes are appealing because they are inexpensive, easy to create and install, heavily used by cavity-nesting birds, and represent an effective tool for engaging the general public in conservation and for creating citizen scientists (Eadie *et al.* 1996, Brossard *et al.* 2012). Nestboxes also are convenient for avian scientists because they can be placed in accessible locations and therefore can form the foundation of a behavioural, ecological or conservation research programme (Møller 1989). As a consequence, nestbox programmes have played a role in research or management for a large number of bird species (Møller 1989, Newton 1994, Eadie & Sherman 1996, Lambrechts *et al.* 2012). Although some nestbox programmes clearly have positive consequences for some species, questions have been raised about their universal effectiveness and possible negative consequences for birds that use them (Schlaepfer *et al.* 2002, Mänd *et al.* 2005, Klein *et al.* 2007, McClure *et al.* 2017). However, the degree to which nestbox programmes are helpful is likely to be context-specific and, although birds in nestboxes have been well studied, there have been only a limited number of comparative empirical assessments of the demographic influence of nestbox programmes.

Red-footed Falcons *Falco vespertinus* have a large distribution that stretches from central Europe through central Asia and into Siberia (Ferguson-Lees & Christie 2001, BirdLife International 2016). In the European Palaearctic, populations of this species are strongly associated with nestbox programmes; outside Europe, they most often breed in nests built by other species. The biology of Red-footed Falcons is poorly known and most studies of this species have been conducted in heavily managed landscapes on the periphery of its range. Furthermore, in central Europe, their populations have declined substantially (Purger 2008, Palatitz *et al.* 2009). As a consequence, the species is currently the focus of conservation efforts built around scientific study and on recovery of breeding populations through the provisioning of large numbers of nestboxes, especially in Hungary (Palatitz *et al.* 2009, Fehérvári *et al.* 2012, Palatitz *et al.* 2015) and Serbia (Purger & Tepavčević 1999, Purger 2008).

Declines of Red-footed Falcon populations in central Europe appear to be driven by reductions of available nest-sites, by pesticide spraying and by the conversion of grasslands to agricultural fields (BirdLife International 2016). In central Europe, for example, these birds occupy areas that have largely been converted to agriculture (> 75% of one province; Purger 2008) and the great majority of breeding pairs studied use nestboxes (Palatitz *et al.* 2015). These changes in habitat and the bird's subsequent responses also reflect global declines both in grassland ecosystems (Hoekstra *et al.* 2005) and in grassland bird populations (Hill *et al.* 2014).

We studied the nesting demography of Red-footed Falcons at a protected area in the core of the species' Palaearctic breeding range. Our goals were to provide basic information on the species' breeding demography in unmanaged or semi-natural landscapes and to evaluate potential natural and anthropogenic drivers of variation of demographic rates. We analysed a 21-year monitoring dataset that we collected in Kazakhstan between 1978 and 2015. Unusually for cavity-nesting birds, this dataset presented the opportunity for us to compare large numbers of nesting attempts in natural nests and in nestboxes. We focused on four demographic parameters associated with the nesting cycle: laying date, the number of eggs produced, the number of fledglings produced, and the number of offspring lost between egg-laying and fledging (offspring loss). We assessed whether there was variation over time in demographic parameters, and how demographic parameters varied in response to three environmental factors (use of human-provided nestboxes, nest location, and if nests were solitary or colonial). We interpret these results in the context of management programmes for this at-risk species.

METHODS

Study area

We monitored Red-footed Falcon breeding biology in and around the Naurzum Zapovednick (National Nature Reserve), in the Naurzum

Region of the Kostanay Oblast (state) of north-central Kazakhstan. The reserve and many of the Red-footed Falcon nests we studied are located in the centre or on the slopes of the Torgay Hollow, an historical wetland draining south from West Siberian Lowlands toward the Aral Sea. Regional climate is continental, dry and windy, with temperatures as low as −45 °C during winter and as high as 41 °C in summer. Average annual temperature is 2.4 °C, and average annual precipitation 233 mm (Katzner *et al.* 2003).

Established in 1931, the Zapovednik encompasses 191 381 ha (Fig. 1) at 51°N, 64°E, approximately at the juncture of the northern Siberian forest and the southern Eurasian steppe. The reserve includes three distinct woodland patches – Tersec, Sip-sin and Naurzum – which make up much of the protected lands (Fig. 1). In the past decade, a larger buffer zone around those forests and wetlands was designated for conservation. About one-third of the core reserve and much of the surrounding buffer zone comprises sandy and mixed soils with feather (*Stipa* spp.) and bunch grasses, or denser clay soils with low sagebrush (*Artemisia* spp.) and other nutrient-rich shrubs and grasses (Formozov 1966). More than 50% of this steppe was ploughed during the failed 'virgin lands' programme initiated in the 1950s. Although many of these formerly farmed fields are now fallow, their outlines are still visible in satellite images, even while they are being recolonized by their original floral and faunal communities (Katzner *et al.* 2003). A small portion of the steppe includes isolated trees and tree rows, often planted to form windbreaks, which are now heavily used by corvids and falcons for nesting.

Focal species

Red-footed Falcons are one of the last migrant raptors to return to breeding grounds in central Kazakhstan each spring. Typical arrival dates are in early May, egg-laying starts about 30 days later, and the incubation and nestling stages both last about 28 days (Bragin 1989). Falcons depart from breeding grounds in early September, and migrate through eastern Europe to the Middle East and then to southern Africa, where they spend the winter (Katzner *et al.* 2016). Return migration is across the Mediterranean and north of the Black Sea (Katzner *et al.* 2016).

Red-footed Falcons are associated with forest-steppe habitat; in general, they nest in trees and forage over grasslands (BirdLife International 2016). At Naurzum, nests are either in human-provided nestboxes or natural, usually usurped or

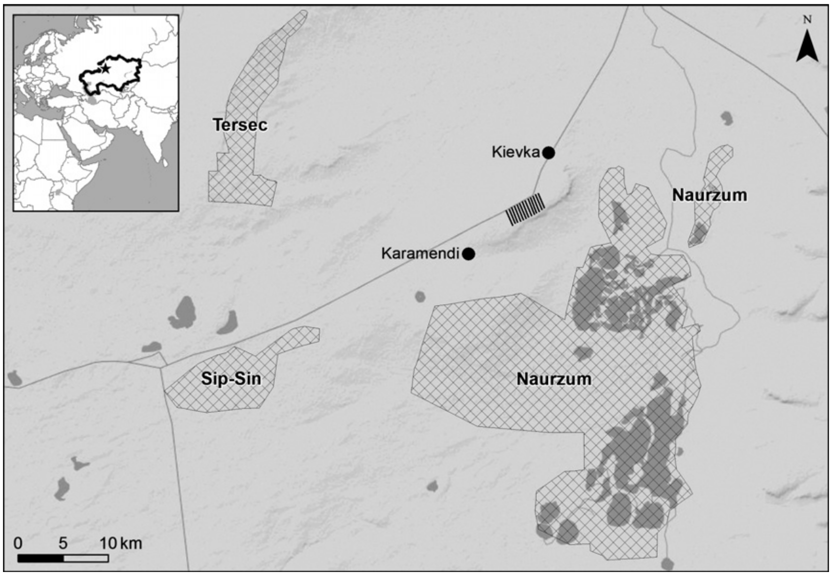

Figure 1. Map of the study area showing the Naurzum Zapovednik (National Nature Reserve), its component regions and the location of the reserve in Eurasia (inset). Red-footed Falcons were studied in all three component regions and in tree rows planted between the villages of Karamendi and Kievka.

abandoned nests of solitary Magpies *Pica pica* and Carrion Crows *Corvus corone* or colonial Rooks *Corvus frugilegus*. Over the 37-year span of our study, Rook populations have declined at the Zapovednik, resulting in fewer opportunities for colonial nesting, and a trend towards solitary nesting by Red-footed Falcons. During the nesting season, Red-footed Falcons forage primarily in grasslands, on insects (especially locusts, Acrididae), reptiles, small birds and mammals (Bragin 1989).

Data collection

Over 21 years between 1978 and 2015 (1978–1989, 1991, 1993 and 2009–2015), we surveyed the Zapovednick and surrounding lands for evidence of breeding by Red-footed Falcons. Surveys were initiated in May, after arrival of the falcons, and at the beginning of the nesting cycle, and extended throughout the breeding period.

Once nests were identified, locations were marked on a map (from 1978 to 1991) or recorded with a GPS (all other years). We described a suite of three environmental factors at each nest: nest type (natural or artificial nestboxes), colonial status (solitary or colonial) and nest location (classified as forest interior or forest edge, the latter including not only true edges but also planted rows of trees in the steppe). At each nest we measured three demographic parameters: laying date (the date on which the clutch was complete), and the numbers of eggs and fledglings produced. To understand the potential drivers of nest failure (as opposed to those that determine number of eggs produced), we also calculated a fourth parameter, offspring loss, defined as the difference between the number of eggs produced and the number of fledglings produced. We also recorded the number of nestlings observed (Table S1). Because it was difficult to standardize timing of visits to count nestlings, we chose not to perform statistical analyses on this parameter.

The number of nests we monitored varied among nesting stages. This was because nests were often found after hatching and because logistical constraints limited our ability to collect data at all stages at all nests. Likewise, because Red-footed Falcons occupy nestboxes or nests that other birds build, it is impossible to identify nesting attempts where eggs were not laid, and thus there were no cases we identified with zero eggs laid. If nests were discovered after a complete clutch was laid, we estimated laying dates based on hatching dates, assuming 28 days between laying and hatching (estimate based on nests where we had information on both laying and hatching). If hatching occurred between two visits, we assumed that the eggs hatched on the middle day of that period. Whenever possible, nests with eggs were revisited multiple times, to verify egg hatching and fledging success rates. The number of fledglings was estimated on the basis of the number of offspring present at approximately 23 days post-hatching (*c.* 80% of the nestling stage; Steenhof & Newton 2007).

Data analysis

To assess variation in demographic parameters over time, we performed two analyses. First, we used generalized linear models (function *glm* in R; R Core Development Team 2014) to test for year-to-year differences in each of the demographic parameters of interest. In these models, year was a categorical variable and we tested for a significant effect of year-to-year variation with either an *F*-test or a chi-square test, as appropriate. Secondly, we tested for directional (linear) trends over time in each demographic parameter by fitting year as a continuous variable. We also tested for skewness in both average annual laying date ($n = 21$ years) and in all estimated and observed laying date data ($n = 633$ nests; function skewness in R package *moments*; Komsta & Novomestky 2015).

To assess how demographic parameters vary in response to environmental factors, we built a series of generalized linear mixed models (GLMMs) fitted with maximum likelihood methods to understand the response of each demographic parameter to variation in categorical environmental factors that we modelled as fixed effects. In each case, we used a standardized protocol to explore our dataset (Zuur *et al.* 2010) and we then built models as follows.

In our models we considered each nesting event to be independent (we did not include a repeated term for the individual birds) but, because our first set of analyses indicated annual variation in demographic factors, we included a categorical random effect for year. We did this because although we know that some ringed falcons have bred in more than 1 year at Naurzum, over the course of this study we only marked about 20 adult falcons and thus we had limited opportunity to track individual breeding birds over time.

Because of the different constraints on, and structures of, the different demographic parameters we measured (e.g. some included zeros, some not), we specified different distributions for each demographic response, based on the characteristics of the data. Each of these distributions required separate R commands and packages (detailed in Table 1).

As we only considered a small number of environmental factors, we evaluated performance of not only the full model (the response variable as a function of fixed effects for nest type, coloniality and nest location), but also the performance of all combinations of sub-models (n = 6) and performance of a null model (intercept only, with random effects but no fixed effects; Doherty *et al.* 2012). We also evaluated the performance of two biologically interpretable interactions among model parameters (nest type * nest location and nest type * coloniality, included only in models with those two terms). We only included models with interactions in the final model set if the interaction term improved performance of the same model without the interaction.

We used Akaike information criterion values corrected for small sample size (AICc) to rank models and estimate model weights (Burnham & Anderson 2002) and we model averaged parameters across all models with full-model averaging to incorporate model selection uncertainty (Buckland *et al.* 1997, Symonds & Moussalli 2011). Model averaging used the R package MuMIn (Bartón 2015).

RESULTS

Breeding biology

We monitored 753 nesting attempts by Red-footed Falcons over the 21 years of our study. Of these, we recorded the laying date for 319 clutches of eggs and we were able to estimate a laying date for an additional 314 cases. Proportion of laying dates observed (not estimated) was similar for natural nests (48%) and for nestboxes (52%). We observed or estimated hatching dates for 422 broods and fledging dates for 256 broods. In total, 80% of nests were classified as solitary (annual range 0–100%), 66% were in nestboxes (annual range 0–100%) and 50% were in forest interior (annual range 0–100%).

Red-footed Falcons laid eggs, on average, on 1 June (±8.40 days; ±sd). Although annual average laying dates were between 22 May and 9 June (Fig. 2a, Table S1a), individual laying dates varied from as early as 11 May to as late as 28 June. Average monitored incubation period was 28.29 days (± 1.02 days; n = 190 clutches). The average hatching date was 30 June (± 8.41 days), annual averages were between 19 June and 9 July, and individual dates varied from as early as 8 June to as late as 25 July. Finally, the average fledge date was 27 July (± 8.62 days), with annual averages varying from 13 July to 2 August and individual dates varying from 11 July to 23 August (Table S1).

Table 1. Model types, distributions specified, and R functions and packages used to evaluate demographic response of Red-footed Falcons to environmental variation in unmanaged forest-steppe in north-central Kazakhstan. Superscripts with R functions and packages indicate the research question addressed where a = evaluation of year-to-year variation in the demographic parameter; b = evaluation of trends over time in the demographic parameter; and c = response of demographic parameter to variation in environmental parameters. If no package is specified, the built-in R function was used. Models were fit with maximum likelihood approximation.

Demographic parameter	Distribution	R Functions	R Package	Reference(s)
Laying date[1]	Gaussian	lm^{a}, glm^{b}, lme^{c}	nlme^{c}	Pinheiro *et al.* (2015)
No. of eggs	Zero-truncated Poisson[2]	glmmadmb^{a,b,c}	glmmADMB^{a,b,c}	Bolker *et al.* (2012)
Offspring loss	Negative binomial[3]	glm.nb^{a,b}, glmer.nb^{c}	MASS^{a,b}, lme4^{c}	Ripley *et al.* (2016), Bates *et al.* (2015)
No. of fledglings	Poisson	glm^{a,b}, glmer^{c}	lme4^{c}	Bates *et al.* (2015)

[1] In models in which laying date was the response variable, laying date was rescaled with the 'scale' function in R, which subtracts the mean (152.15) and divides by the standard deviation (8.40). [2] We were unable to identify breeding attempts that failed before egg-laying and thus there are no zeros in the egg data, hence the use of this distribution. [3] Poisson models suggested overdispersion, hence the use of the negative binomial distribution.

Laying date varied both among years and within years (Fig. 2a). The distribution of average annual laying dates was not highly skewed (skewness = −0.2455; Fig. 3a). However, the distribution of laying dates combined over the 37 years of this study was positively skewed (skewness = 0.4195; Fig. 3b), suggesting that of the nests monitored, late laying dates were proportionately more frequently observed than were early laying dates.

On average, Red-footed Falcons laid 3.56 ± 0.67 (± sd) eggs per clutch (Fig. 2b, Table S1a). All clutches had between one and five eggs, except for a single clutch laid in a nestbox in 1998 that had six eggs. Nests produced up to five nestlings (mean 2.94 ± 1.24). On average, 1.31 ± 1.38 offspring were lost per nest (range 0–5) and up to five nestlings fledged (mean 2.29 ± 1.35; Fig 2d).

Inter-annual variation in demographic rates

We detected substantial year-to-year variation in most demographic rates. In particular, we observed significant inter-annual differences in laying date ($F_{20,612} = 14.198$, $P < 0.001$), offspring loss ($\chi^2_{20} = 34.424$, $P = 0.023$) and number of fledglings produced ($\chi^2_{20} = 32.953$, $P = 0.034$). We observed no inter-annual differences in the number of eggs produced ($\chi^2_{20} = 10.216$, $P = 0.964$).

We detected no evidence in our 620 nesting attempts of long-term directional (linear) trends in laying date ($F_1 = 1.02$, $P = 0.312$) or the number of eggs produced ($\chi^2_1 = 0.156$, $P = 0.693$). There was weak evidence of a decrease over time in number of fledglings produced ($\chi^2_1 = 3.651$, $P = 0.056$), and strong evidence for an increase over time in offspring loss ($\chi^2_1 = 5.897$, $P = 0.015$).

Drivers of variation in demographic rates

Of the models describing variation in laying date, those with a term for nest type included 98% of the model weights (Tables 2 & S2). The estimate for the nestbox parameter was non-zero, and all other model parameters were uninformative (i.e. confidence intervals for these parameters included zero; Arnold 2010). The model with the most support in the data had a single fixed effect of nest type (41% of weight in our model set; Table 2, Fig. 4a). The second most highly supported model was one with both a fixed effect of nest type and a fixed effect of coloniality (28% of support in the data) and the third, a model with fixed effects of nest type and nest location (17% of support in the data). Models with a term for nest type always performed better than models without such a term, and ΔAICc between the best and worst models was 11.55. Models with interaction terms did not perform as well as similar models without the interaction term. Model averaged estimates suggested that using a natural nest instead of a nestbox changed laying date by −2.01 ± 0.70 (se) days (i.e. laying dates in a colony on a forest edge were 2 days earlier in nestboxes than in a natural nest). Similar patterns were also evident using empirical means, where nestboxes, especially those on forest edges, had slightly earlier laying dates than did natural nests (Fig. 4a).

No single model explained a large amount of the variation in egg production by Red-footed Falcons (Tables 2 & S2). In this case, the null model (with a random effect for year) had the most support in the data. Of the remaining models, once again, the model with the most support in the data included only a term for nest type (17% of weight in the model set; Table 2, Fig. 3b). However, in this case, models with the second and third most support in the data had AICc weights nearly equivalent to each other and included either a single term for nest location or coloniality. All models in the model set were separated by a maximum ΔAIC of 5.59 and models with interactions performed poorly. There were no informative model parameters in the final model-averaged coefficients. Similar patterns were also evident in empirical means, with essentially no differences in egg production regardless of the type, coloniality or nest location (Fig. 4b).

The best model describing variation in offspring loss had 64% of the support in the data (Tables 2 & S2). This model had three terms: nest type, nest location and an interaction between those two parameters (Table 2, Fig. 4c). The only other model with > 10% of the support in the data was the same as the first model but without the interaction term. Model-averaged estimates suggested that the lowest offspring loss was in a natural nest and that switching to a nestbox on a forest edge increased offspring loss by 0.39 ± 0.20 (i.e. in a colony on a forest edge, more offspring died in a nestbox than in a natural nest). There were no

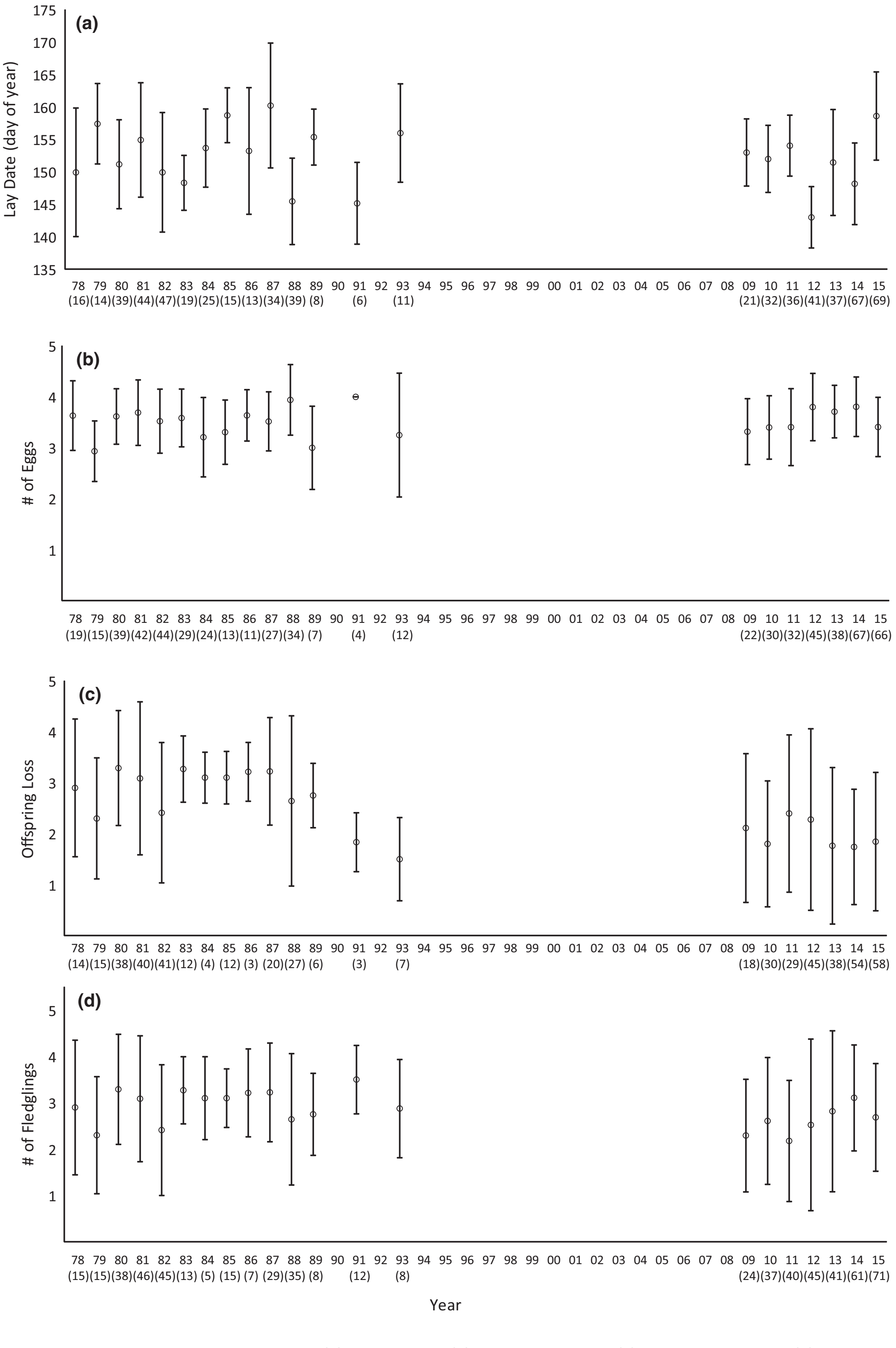

Figure 2. Annual mean and standard deviation of (a) laying date, (b) number of eggs, (c) offspring loss and (d) number of fledglings measured from Red-footed Falcon nests monitored for 21 years between 1978 and 2015 at the Naurzum Zapovednick, Kazakhstan. Numbers in parentheses on the *y*-axis indicate number of nests considered in each year.

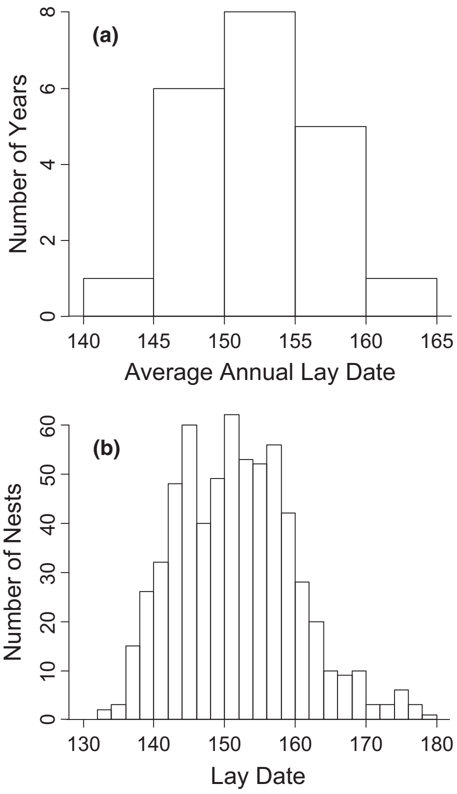

Figure 3. Histograms showing (a) annual average of laying date ($n = 21$ years), and (b) all measurements of dates on which eggs were laid ($n = 633$ estimated and monitored egg-laying events) for Red-footed Falcons at the Naurzum Zapovednik, Kazakhstan, monitored for 21 years between 1978 and 2015.

other informative model parameters in the final averaged model. These patterns were evident in the empirical means, which showed a substantial increase in offspring loss in nestboxes on forest edges (Fig. 4c).

The best model describing variation in numbers of fledglings produced had 80% of the support in the data and was separated from the second model by a ΔAICc of 5.13 (Tables 2 & S2). This first model again included terms for nest type, nest location and an interaction between the two parameters (Table 2, Fig. 4d). No other model had > 6.2% of the support in the data. Model-averaged estimates suggested that the greatest number of fledglings were in a natural nest on a forest edge, and that moving to a nestbox on a forest edge resulted in a substantial decrease in fledgling production (−0.24 ± 0.12). There were no other informative model parameters. Finally, these patterns were again evident in the empirical means, which showed a noticeable decrease in fledgling production in nestboxes on forest edges (Fig. 4d).

DISCUSSION

Nestboxes are a widespread, cost-effective conservation tool whose implementation has multiple benefits for birds, science and society. Use of nestboxes in this study allowed us to gather a far greater number of measurements on falcon demography, with concomitant increases in the strength of our inference, than would otherwise be possible. Uniquely to this field site, it also allowed us to explore the consequences to birds of nesting in a variety of different settings and the potential for unexpected demographic effects (Schlaepfer *et al.* 2002, Robertson & Hutto 2006) that Red-footed Falcons faced by using certain types of nestboxes. These potential effects are likely to be of limited consequence for the viability of this large and apparently stable population, especially in light of threats to adult survivorship they may experience elsewhere (Katzner *et al.* 2016). However, if offspring loss is higher in some nestboxes in heavily managed landscapes on the periphery of the species' range, where populations are less robust, it could have important consequences for demography and conservation.

Drivers of Red-footed Falcon demography

There are several striking features of the demographic parameters we assessed in this Red-footed Falcon population. Given the relatively low within-year variability in laying dates, the positive skew we documented in the overall distribution of all laying dates (Fig. 3b) can be produced by one of two processes. The first would occur when there is a larger number of years in which egg-laying is late. This is unlikely, as we also know that average annual laying dates had a small negative skew, suggesting that at an annual scale, early laying is slightly more common than is late laying (Fig. 3a). Alternatively, and apparently more likely, this pattern could occur if, within a given year, a small subset of birds lay later than would be expected. A plausible explanation for this pattern is that Red-footed Falcons sometimes lay second clutches. Although second clutches have not been conclusively documented for this species, other small falcon species are known to lay second

Table 2. Selection tables for models describing drivers of reproductive performance of Red-footed Falcons in unmanaged forest-steppe in north-central Kazakhstan. Data on reproduction were collected from 753 nesting events over 21 years between 1978 and 2015. We used linear mixed effects model (see Table 1 for details of models) with maximum likelihood methods for model estimation and ranked models by Akaike's information criterion values corrected for small sample sizes (AICc). Fixed effects in our models included nest location (forest-interior or grassland/forest edge), degree of coloniality (solitary or colonial) and nest type (natural nest or nestbox) and two biologically relevant interaction terms (nest type * nest location and nest type * coloniality). Interaction terms were considered in all model sets but were only reported and considered in the two of the four final model sets where inclusion improved model performance. All models also included a random effect for year. Degrees of freedom differ among model sets because the models specified were different for each model set.

	Model	df	logLikelihood	AICc	Weights
Laying date	Nest type	4	−806.54	1621.15	0.413
	Nest type + coloniality	5	−805.90	1621.89	0.285
	Nest type + nest location	5	−806.44	1622.97	0.166
	Nest type + nest location + coloniality	6	−805.75	1623.63	0.120
	Coloniality	4	−810.47	1629.00	0.008
	Intercept only	3	−812.32	1630.68	0.004
	Nest location + coloniality	5	−810.42	1630.94	0.003
	Nest location	4	−812.32	1632.70	0.001
No. of eggs	Intercept only	2	−995.36	1994.74	0.369
	Nest type	3	−995.15	1996.33	0.166
	Nest location	3	−995.36	1996.75	0.135
	Coloniality	3	−995.36	1996.76	0.135
	Nest type + nest location	4	−995.12	1998.31	0.062
	Nest type + coloniality	4	−995.13	1998.33	0.061
	Nest location + coloniality	4	−995.35	1998.77	0.049
	Nest type + nest location + coloniality	5	−995.12	2000.33	0.023
Offspring loss	Nest type + nest location + nest type * nest location	6	−791.44	1595.04	0.644
	Nest type + nest location	5	−793.78	1597.68	0.172
	Nest type + nest location + coloniality	6	−793.73	1599.63	0.065
	Nest type	4	−796.26	1600.61	0.040
	Nest location	4	−796.66	1601.40	0.027
	Nest type + coloniality	5	−795.82	1601.76	0.022
	Intercept only	3	−798.31	1602.67	0.014
	Nest location + coloniality	5	−796.66	1603.43	0.010
	Coloniality	4	−798.11	1604.30	0.006
No. of fledglings	Nest type + nest location + nest type * nest location	5	−1063.35	2136.80	0.800
	Nest type + nest location	4	−1066.93	2141.93	0.062
	Nest location	3	−1068.40	2142.83	0.039
	Nest type + nest location + coloniality	5	−1066.72	2143.53	0.028
	Intercept only	2	−1070.20	2144.42	0.018
	Nest type	3	−1069.22	2144.48	0.017
	Nest location + coloniality	4	−1068.35	2144.76	0.015
	Nest type + coloniality	4	−1068.51	2145.10	0.013
	Coloniality	3	−1069.83	2145.70	0.009

clutches (Katzner *et al.* 2005), either when conditions are good for producing two broods or when a first clutch fails.

Our statistical models (Table 2) suggested that birds in nestboxes laid eggs earlier. However, no single model had strong support in the data, suggesting that variation in laying date is driven at least in part by factors we did not evaluate here that fluctuate among years and that influence all birds in similar manners. The most likely candidate for this factor is weather – on wintering grounds, during migration and even on arrival – and there is good evidence for such relationships in populations of other bird species (Sergio 2003, Visser & Sanz 2009, Visser *et al.* 2009). We suspect that a more comprehensive dataset that linked these factors to variation in individual quality would allow creation of models that more effectively described variation in laying date.

In contrast, the number of eggs produced showed no differences among years and comparatively greater within-year variability (Fig. 2). Likewise, our statistical models demonstrated that none of the

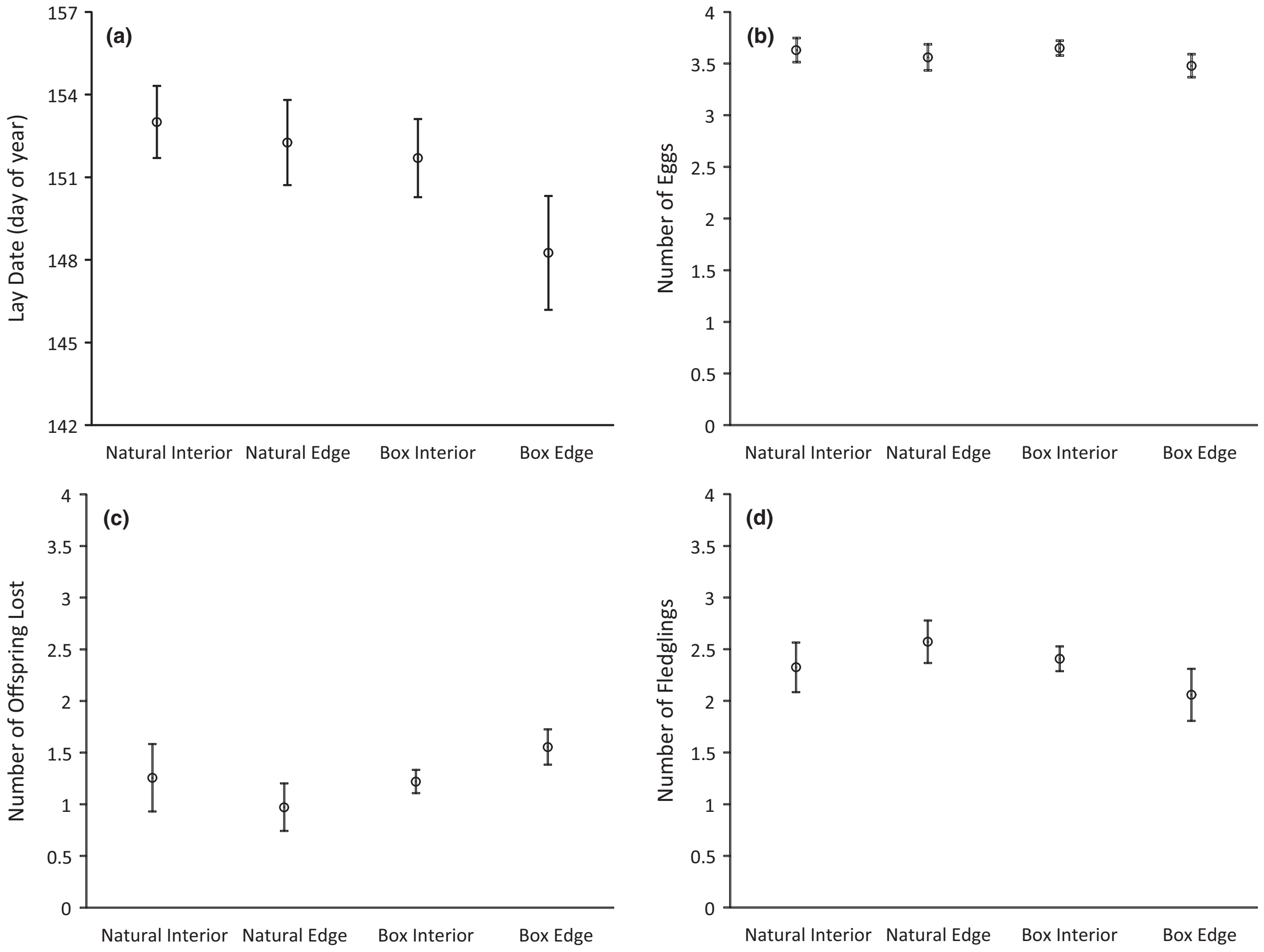

Figure 4. Empirical grand means (average of means from within each year) showing interactive effects of nest type and nest location reproduction of Red-footed Falcons monitored for 21 years between 1978 and 2015 at the Naurzum Zapovednik, Kazakhstan. Interactions had no explanatory value on variation of either (a) laying date or (b) number of eggs laid, but they explained substantial variation in (c) number of fledglings produced and in (d) offspring loss.

environmental factors we considered explained much variation in egg-laying (Table 2). Such patterns make sense if variation in egg production is determined not by factors that affect the entire population but by among-individual variation that is independent of local conditions, such as in quality, environmental contaminants or condition upon arrival at breeding grounds (Negro *et al.* 1993, Lescroël *et al.* 2009, Zabala & Zuberogoitia 2014).

Finally, offspring loss and number of fledglings were different from the other two demographic parameters in that they were variable both across years and within years (Fig. 3) and variation in these parameters was best explained by nest type, nest location and an interaction between the two. As such, these parameters are likely to be influenced by a combination of both among-individual variation (as was the case for egg production) and across-population factors (as was the case for laying date). These analyses suggest that individual condition or quality is likely to interact with patterns in variation in prey availability (Steenhof *et al.* 1997, Salafsky *et al.* 2007) or the occurrence of severe storms that could cause nest failure (Fisher *et al.* 2015) to drive offspring loss and, ultimately, the number of fledglings produced.

Demographic consequences of nestbox use by falcons

The increase in offspring loss in nestboxes and the importance of an interaction between nest type and nest location illustrate the potential for unexpected consequences of conservation actions for Red-footed Falcons (Table 2, Fig. 4). We found good evidence that laying dates were earlier in nestboxes than in natural nests (Fig. 4a, Tables S1b & S2a). We also found strong evidence that the subset of these nestboxes on forest edges have higher offspring loss and, consequentially, lower output of fledglings (Fig. 4c, Tables S1b & S2c).

Studies of other species suggest that early nesters tend to be dominant individuals that arrive on the nesting grounds earlier and in better condition than their peers (Marra *et al.* 1998, Harrison *et al.* 2011). If the Red-footed Falcons that nested in certain nestboxes and had higher offspring loss are also those that are dominant and in better condition, they may have ended up in an ecological trap that depressed their reproductive success. Nestboxes are known to have similar demographic effects in other settings. In Estonia, Great Tits *Parus major* that nested in boxes in food-rich deciduous forest laid earlier and produced larger clutches, but those that nested in boxes in coniferous forest fledged more young that had higher return rates (Mänd *et al.* 2005). Similarly, ducks of several species have lower reproductive success in nestboxes because of density dependence or higher brood parasitism (Schlaepfer *et al.* 2002, Mänd *et al.* 2005) and Barn Owls *Tyto alba* hatched in nestboxes had lower survival than those hatched in church towers without boxes (Klein *et al.* 2007). Finally, American Kestrels *Falco sparverius* nesting in boxes disturbed by humans had higher failure rates, in spite of the better potential prey resources available to them (Strasser & Heath 2013).

Although the functional cause of the difference in laying date and the higher offspring loss at certain nestboxes at Naurzum is unclear, there are several possible explanations: (1) a potential increase in predation rates at artificial nests on edges, (2) overheating in unventilated nestboxes exposed to greater sunlight on edges than in the interior, and (3) fluctuations in habitat quality such that edge habitats are better earlier in the season but become lower quality during the rearing phase. There is evidence from other systems to support all three of these explanations. For example, it is well documented that predation rates on bird nests are higher in fragmented edge habitats (Robinson *et al.* 1995), and it may be that nestboxes that are built to be accessible to humans may also be relatively more accessible to predators. Likewise, although nestboxes provide protection from rain, their walls are thinner than similar natural cavities and they are less well ventilated than an exposed corvid nest. As such, temperatures inside nestboxes may fluctuate more than in a thick-walled natural cavity and may be higher than in a wind-blown corvid nest. Such temperature variation could increase nestling mortality rates. Finally, seasonal changes in habitat quality can vary by location (i.e. a site that appears high quality early in the season may become low quality later in the season) with demonstrated consequences for certain species (Watson 2011).

Of the 39 global members of the genus *Falco*, at least 12 are considered conservation-reliant and threatened by population declines of some type (Scott *et al.* 2005, BirdLife International 2016). Many of these, including American, Common, Lesser and Mauritius Kestrels (*Falco sparverius*, *F. tinnunculus*, *F. naumanni* and *F. punctatus*, respectively), are or have been supported by nestbox programmes, and in many cases those programmes have been essential to the recovery of the species. Nevertheless, our analyses identify interactions that lower reproductive output of some birds that use nestboxes. Such circumstances may have minimal short-term relevance in transformed landscapes where nestboxes are the only good option to supplement breeding opportunities (e.g. Red-footed Falcons in central Europe). However, if nestboxes in other settings can lead to depressed reproductive success, it may mean that they are less than ideal as a universal long-term solution to conservation problems for cavity-nesting birds.

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SUPPORTING INFORMATION

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

Table S1. Demographic parameters for Red-footed Falcons breeding at the Naurzum Zapovednik, Kazakhstan, monitored for 21 years between 1978 and 2015.

Table S2. Model-averaged coefficient estimates, unadjusted standard errors and parameter significance tests for models describing demography of Red-footed Falcons breeding at the Naurzum Zapovednik, Kazakhstan, monitored for 21 years between 1978 and 2015.