

Nesting ecology of solitary-nesting Amur Falcons (*Falco amurensis*) in central Mongolia

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ABSTRACT. Amur Falcons (*Falco amurensis*) are a migratory species that face a variety of threats across their range, but little is known about their breeding ecology. These falcons breed in forest habitats in Eastern and Central Asia using nests constructed by corvids, including Eurasian Magpies (*Pica pica*). We monitored nests of 21 pairs of Amur Falcons at Hustai National Park in central Mongolia in 2017. Our objectives were to describe their basic nesting ecology, estimate nest survival by modeling the daily survival rate (DSR), examine nest selection by modeling it as a function of nest and site covariates, and use a spatial simulation to test hypotheses concerning intra- and interspecific avoidance. Clutch sizes averaged 4.1 eggs ($N = 21$ nests), and incubation and nestling periods averaged 25.7 and 26.1 d, respectively. The daily survival rate was 0.98, with young in 12 nests surviving to fledging. Nest structures were more likely to be selected as percent cover of nest bowls increased, usually in the form of a dome of sticks with multiple side entrances. Closed nests likely provide increased protection from predators. In contrast to congeneric Red-footed Falcons (*F. vespertinus*) that nest in large colonies, Amur Falcons nested no farther from or closer to nests of either conspecifics or congeners than expected by chance. One factor likely contributing to this difference is that Red-footed Falcons often use the nests of colonial-nesting Rooks (*Corvus frugilegus*), whereas Amur Falcons typically use the nests of non-colonial Eurasian Magpies. The ongoing loss of deciduous trees like white birch (*Betula platyphylla*) across the breeding range of Amur Falcons, probably due to climate change and increased grazing pressure, is likely to reduce the availability of nesting habitat for Eurasian Magpies which, in turn, will likely reduce availability of nests for Amur Falcons and other small falcons.

RESUMEN. **Ecología de la anidación de los halcones *Falco amurensis* que anidan en solitario en Mongolia central.**

El halcón *Falco amurensis* es una especie migratoria que enfrenta una variedad de amenazas a lo ancho de su rango, si bien se sabe poco de la ecología de su anidación. Estos halcones anidan en hábitats boscosos en Asia central y oriental utilizando nidos construidos por córvidos, incluida la urraca *Pica pica*. Monitoreamos los nidos de 21 pares de *F. amurensis* en Hustai National Park en Mongolia central en 2017. Nuestros objetivos fueron describir la ecología básica de su anidación, estimar la supervivencia de sus nidos modelando la tasa diaria de supervivencia (DSR), examinar la selección de nidos modelándolos como función de covariables de nidos y sitios, y usar una simulación espacial para someter a prueba hipótesis relacionadas con la evasión intra e interespecífica. Los tamaños de puesta promediaron 4.1 huevos ($N = 21$ nidos), y los periodos de incubación y de crianza de polluelos promediaron 25.7 y 26.1 días respectivamente. La tasa de supervivencia diaria fue 0.98, con polluelos de 12 nidos sobreviviendo hasta la emancipación. Las estructuras nido fueron más proclives a ser seleccionadas según el porcentaje de cobertura del nido en forma de tazón, usualmente domos de varitas con múltiples entradas laterales. Los nidos cerrados probablemente incrementan la protección de depredadores. En contraste con su congénico, el halcón *F. vespertinus* que anida en grandes colonias, *F. amurensis* anidó no más lejos o más cerca de conespecíficos o congénicos de lo esperado aleatoriamente. Un factor que posiblemente contribuye a estas diferencias es que *F. vespertinus* frecuentemente usa los nidos de

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la graja *Corvus frugilegus* que anida en colonias, mientras que *F. amurensis* típicamente usa los nidos de la urraca no-colonial *P. pica*. La pérdida en marcha de árboles deciduos como el abedul *Betula platyphylla* a lo ancho del rango reproductivo de *F. amurensis*, probablemente debida al cambio climático, y el incremento en la presión de pastoreo, posiblemente reducen la disponibilidad de hábitat de anidación de *P. pica* que, a su vez, resulta en una reducción en la disponibilidad de nidos para *F. amurensis* y otros halcones pequeños.

Key words: *Betula platyphylla*, colonial nesting, daily survival rate, Eurasian Magpie, Hustai National Park, nest-site selection, *Pica pica*, spatial simulation

Amur Falcons (*Falco amurensis*) are small, migratory falcons that breed in southeastern Siberia, central and eastern Mongolia, north-eastern China, and North Korea (White et al. 1994). These falcons migrate to wintering areas in southern Africa via India (Dalvi et al. 2013), undertaking the longest known over-water migration of any bird of prey (Meyburg et al. 2017). Basic nesting habits, chronology, and diet of this species are known from several studies in Mongolia (Schäfer 2003, Stubbe et al. 2010, Usukhjargal et al. 2012, Wang and Gombobaatar 2012, Bayasgalantselmegeg 2015, Gombobaatar et al. 2017).

Amur Falcons nest primarily in old or co-opted nest structures built by corvids such as Eurasian Magpies (*Pica pica*) and Rooks (*Corvus frugilegus*). They lay an average of four eggs that are incubated by both females and males for about 27 d (Schäfer 2003, Stubbe et al. 2010), broadly similar to American Kestrels (*F. sparverius*) and Common Kestrels (*F. tinnunculus*), except that male Common Kestrels are not known to incubate (White et al. 1994). Apparent nest success has been found to be between 73 and 79% at several sites (Schäfer 2003, Gombobaatar et al. 2017). However, non-biased model-based nest survival estimates (Brown et al. 2013) that are important for comparisons among sites or species are not available for Amur Falcons. Additionally, selection of nest structures and nesting sites has been found to be important for the breeding success of American Kestrels (Greenwood and Dawson 2011, Touihri et al. 2019), Lesser Kestrels (*F. naumanni*) (Bobek et al. 2018), Common Kestrels (Rodríguez et al. 2018), and Red-footed Falcons (*F. vespertinus*) (Kotymán et al. 2015), but this has not been evaluated for Amur Falcons.

Amur Falcons typically occupy only 10–15% of the available corvid nests in their breeding areas (Schäfer 2003), suggesting that they make choices based on both the

characteristics and location of nests. The spatial distribution of conspecific nests is interesting because falcons display a range of nesting strategies from solitary to colonial, the causes of which are not known (Cecere et al. 2018). American Kestrels, for example, typically nest at least 800 m from conspecifics (Rohrbaugh and Yahner 1997), whereas Red-footed Falcons, sister species of Amur Falcons (Fuchs et al. 2015), often nest in dense colonies in the old nests of colonial-nesting Rooks (Purger and Tepavčević 1999, Kotymán et al. 2015). Another pair of closely related pair of species, Common Kestrels and Lesser Kestrels (Fuchs et al. 2015), display a similar contrast in strategies; the former is typically solitary, whereas the latter is a colony nester (White et al. 1994). Amur Falcons nest closer to each other (5–200+ m; Schäfer 2003) than solitary and territorial American Kestrels, but farther from conspecifics than truly colonial species.

Colonial nesting is often thought to be advantageous for information sharing (the Information Center hypothesis) in cases where food resources are abundant yet ephemeral, which is thought to be more commonly the case for insectivorous birds than those that feed on mammals and other birds (Ristow 2004, Cecere et al. 2018). Common and Lesser kestrels, which feed primarily on mammals and insects, respectively, fit this hypothesis well, but Amur and Red-footed falcons seem to be equally insectivorous (Fülöp and Szlivka 1988, Schäfer 2003, Alexander and Symes 2016). However, determining whether Amur Falcons actively choose to nest farther from (or closer to) conspecifics, or are simply using available nest structures that are most suitable, requires information about the spatial distribution of potential nest structures.

We monitored the nests of Amur Falcons in Hustai National Park (HNP), Mongolia, as well as both active and unused nests of Eurasian Magpies, and report on their basic breeding ecology. To estimate the average

daily survival rate (DSR) of eggs and nestlings, and determine how falcons selected nest structures, we used linear models based on nest and site covariates. We also used a spatial simulation, incorporating the results of nest-structure selection models, to determine whether patterns of intraspecific Amur Falcon nest spacing are a function of active choice, or are simply constrained by nest structure availability or the active nests of Eurasian Magpies and other small falcons. All of these are considered in addressing the implications of ongoing tree die-offs for Amur Falcons in the steppe ecosystem.

METHODS

Study area. Our study was conducted in Hustai National Park (HNP), a 570-km² protected area located 100 km west of Ulaanbaatar, Mongolia (47.764°N, 105.879°E), in the Eurasian Steppe. It was established in 2003 as a reintroduction site for endangered Przewalski's horses (*Equus przewalskii*) so there are no livestock in the area and there are substantial populations of native ungulates and other wildlife (Yoshihara et al. 2010, Dorj and Namkhai 2013). Most of the park consists of steppe grassland, but 5% is covered by patches of white birch (*Betula platyphylla*) and Eurasian aspen (*Populus tremula*), both of which have suffered > 10% die-offs in recent years (Bayarsaikhan et al. 2009, Hoshino et al. 2018).

We monitored nests of Amur Falcons and Eurasian Magpies from 17 June to 14 August 2017, in a 6-km² section of several adjacent drainages in the park. This area consisted mainly of gently sloping open birch forests interspersed with grasslands (Fig. 1A).

Nest monitoring. Amur Falcons nest in old or co-opted stick nests built by Eurasian Magpies that are easily detected in the relatively sparse foliage of birch trees (Fig. 1B). Typical nests are balls of sticks ~ 0.6 m in diameter with one or more entrances to a center cavity. We assigned each nest structure in the study area a number and marked its location with a Garmin GPS unit. We checked each nest for eggs or nestlings during the second and fourth weeks of June throughout most of the study area. In the northwestern section of the study area (north of 47.72°N), however, we did not climb to

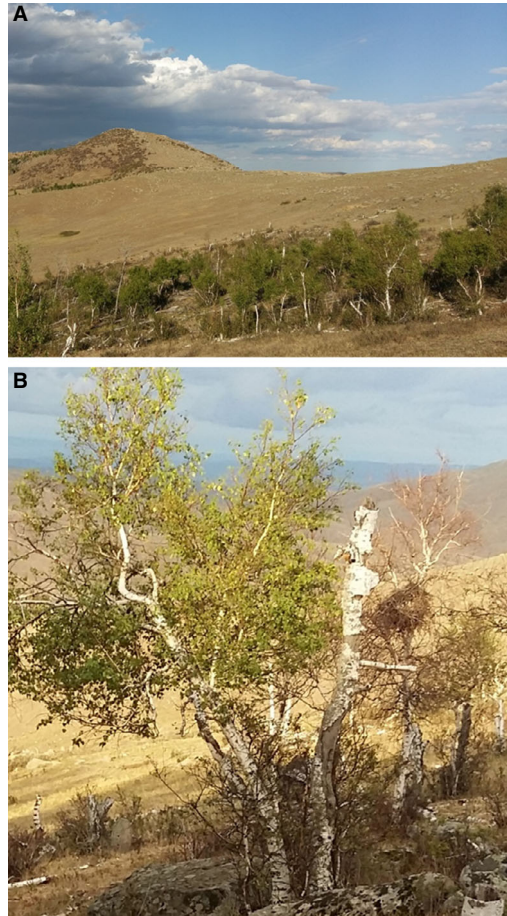


Fig. 1. Stands of white birch (*Betula platyphylla*) in the steppe landscape of Hustai National Park in Mongolia (A), and a typical nest structure built by Eurasian Magpies (B). These stands of birch are important for magpies and many species that use their nest structures, including Amur Falcons. Photos by R. Burner. [Color figure can be viewed at wileyonlinelibrary.com]

nests, but tapped on trees in an attempt to flush adults that may have been present, and climbed to nests only when adults were observed in the area. For each nest structure, we recorded height above ground, diameter, distance to forest edge (the outermost trees in the patch of trees, if any), distance to edge of tree, percent of the nest bowl covered by the nest structure when viewed from above (estimated by eye), percent of ball obscured by tree foliage as viewed from the ground when 20 m from the tree (estimated by eye from two perpendicular angles and averaged), and

the condition of the ball. We categorized nest condition as (i) like-new with some still-green sticks, (ii) fully intact, but dried out, (iii) intact, but missing some sticks, (iv) lost many sticks, but with a useable though sometimes slanted platform, or (v) falling apart and lacking a stable platform.

For each active nest, we recorded the number of eggs or nestlings. For each Amur Falcon nest with eggs, two eggs were floated briefly in a small jar of water. Float height above water was measured with a ruler, and angle was estimated by eye. For the few nests where neither laying nor hatching were observed, float data were compared with known-age nests to estimate nest initiation dates.

Nests were monitored every 3 d until they either failed (nestlings or eggs disappeared or were killed/destroyed) or young fledged. Nestlings approaching fledging age typically left nests and perched on nearby branches and sometimes flew away when we approached nests. Nests were considered to have fledged young if young were observed to fly away, or if nestlings of sufficient age and feather development (i.e., able to fly) were present and outside the nest on the visit prior to it being discovered empty, and in the absence of signs of predation (i.e., scattered feathers). For purposes of nest survival analyses, the last day of exposure on successful nests was the day of the last visit when full-size young were present outside the nest. For nests that failed on an unknown day between the final two checks of a nest, the nest survival models estimate the failure date in that time period.

Data analysis. To estimate Amur Falcon nest survival, we used the package “RMark” (Laake 2013) in R (R Core Team 2018) to run a set of models in MARK (White and Burnham 1999) that we deemed biologically plausible. These included additive effects of date, nest age (as estimated based on hatch date, if available, or egg float observations), nest stage (incubation vs. nestling), nest bowl percent cover, and distance to forest edge. All covariates had variance inflation factor (VIF) values of < 1.8 , indicating a lack of covariance. We used AIC_c model selection and the “covariate.predictions” function to estimate an average daily survival rate. DSR is less biased than apparent survival, partly because it accounts for the fact that many nests are

discovered sometime after nest initiation (Brown et al. 2013).

Amur Falcons used only a fraction of the available nest structures in any given season, and we used generalized linear models to determine the characteristics of nests that were selected. All nest and site covariate data were scaled to a mean of zero and standard deviation of zero. We used “glmulti” to run models to predict nest use by Amur Falcons. Models included all combinations of nest height, nest ball diameter, tree cover, nest bowl percent cover, distance to forest edge, nest condition, and distance to the edge of nest tree and their additive effects. Several of these covariates have been found to be important for other Mongolian raptors (Gombobaatar et al. 2010, 2012). All covariates were scaled to have a mean of zero and a standard deviation of one. AIC_c model selection (Burnham et al. 2011) was used to rank the models, and model-averaged covariates were estimated using the “coef” function. For covariates that were important in the model, we also report mean values for used and unused nests and test differences using *t*-tests.

To determine whether Amur Falcons selected nest sites based on proximity to the nests of conspecifics, members of the same genus, or Eurasian Magpies, potential nest predators given their appetite for eggs of passerines and partridges (Madden et al. 2015), we used locations of nests as determined with a GPS unit to calculate the distance from each nest to the nearest conspecific and magpie nests. To generate a null expectation for comparing these values, we then conducted 1000 simulations where the same number of Amur Falcon nests was randomly distributed among the total available nest structures in the study site. Not all nests were equally suitable for the falcons so the probability of a nest being occupied in the simulations was proportional to its probability of being occupied based on output from our top nest-structure selection model, as described above. Eurasian Magpies initiate nests several weeks before Amur Falcons and so are already nesting when pairs of falcons choose nest locations. For analysis of distances to magpie nests, nests in the northwestern section of our study area (north of 47.72°N) were excluded because we did not climb to every nest structure and likely failed to find

some active magpie nests in this area. R code for the simulations is available in Appendices S1 and S2. Values are reported as means \pm SE, unless indicated otherwise.

RESULTS

We examined 223 nest structures (Fig. 2); 50 were active nests, including 21 Amur Falcon (Table S1) and 22 Eurasian Magpie nests. Amur Falcons occupied 9% of the available nest structures (Table S2). Observed nesting densities in our 6-km² study area were 3.5/km² for Amur Falcons, 3.7/km² for Eurasian Magpies, and 1.2/km² for other species. One Amur Falcon nest was in a tree that was difficult to climb so its fate was unknown and it was excluded from our survival analyses.

Median nest initiation date (Table S1) for Amur Falcons was 10 June (range = 1 June–25 June). Clutch sizes averaged 4.1 \pm 0.4 eggs (N = 21 nests). During the laying period, eggs were laid every 1–3 d. Incubation and nestling periods averaged 25.7 \pm

2.0 and 26.1 \pm 0.3 d (95% CI), respectively. Measurements of nestlings are provided in Table S3.

Nests used by Amur Falcons were an average of 4.0 \pm 0.2 m above ground, 23 \pm 5% obscured by foliage, and had nest bowls that were 74 \pm 5% covered. Occupied falcon nests averaged 0.60 \pm 0.02 m in diameter, 13.1 \pm 3.7 m from forest edges, and 0.5 \pm 0.1 m from the edge of nest trees. On a 1–5 scale of nest condition (one being fully intact, in like-new condition), the average nest score was 2.2 (Table S4; characteristics of the nests of other species and unoccupied nest structures are provided in Table S2).

Eurasian Magpies were already incubating eggs when our study began. The 15 nests we monitored had an average clutch size of 5.3 \pm 0.5 eggs (95% CI). Hatch dates ranged from ~ 4 June to 1 July, with a median date of 15 June. All eggs hatched in these 15 nests, and an average of 4.0 \pm 0.5 young (95% CI) fledged from successful nests (N = 11). The apparent nest success rate for

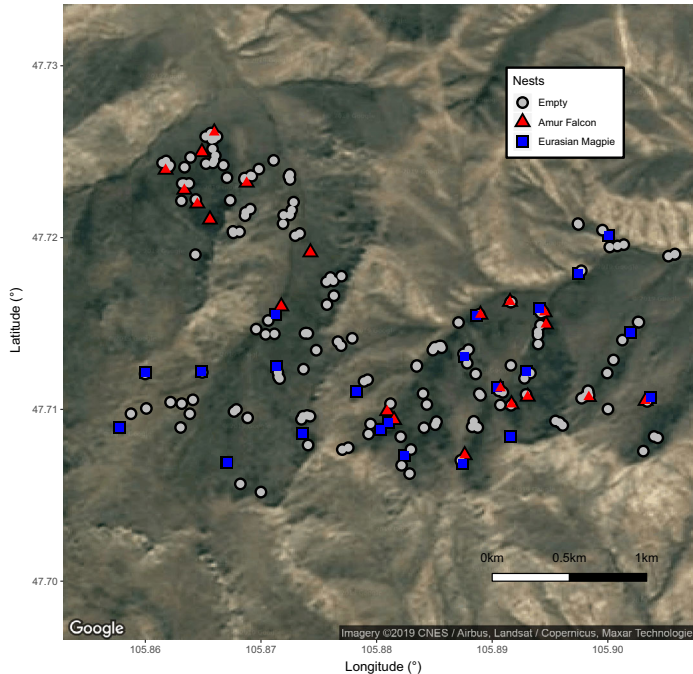


Fig. 2. Map of active and inactive nest structures in Hustai National Park in central Mongolia from Google Earth. Nest searching in the northwestern portion of the study site was late enough in the season that Eurasian Magpies would not have been reliably detected, and so this area was excluded from falcon-magpie spatial co-occurrence analyses. [Color figure can be viewed at wileyonlinelibrary.com]

Eurasian Magpies was thus 73%. We did not calculate DSR for Eurasian Magpie nests because of a lack of data from early in their nesting period (before our falcon study began).

Nest survival. The nest survival rate of Amur Falcons did not vary significantly with nest age, nest initiation date, nest stage (incubation vs. nestling), nest bowl percent cover, or distance to forest edge. A model assuming a single constant survival rate performed best according to AIC_c scores (Table 1). Average daily survival rate (DSR) was 98.1% (95% CI = 0.970–0.992) based on the best model of a constant survival rate. This survival rate, applied across the average laying, incubation, and nestling periods, would result in 31.6% of initiated nests surviving to fledging (95% CI = 0.085–0.519). Of 20 falcon nests where the final fate was known, at least one young fledged from 12 (60%). This apparent nest survival estimate is much higher than our model-estimated nest survival rate because some nests in our study were discovered in the late incubation or nestling stages, biasing the apparent survival estimate upwards. Of eight nests that failed, one failed during the laying stage (apparently abandoned), four during incubation (eggs disappeared), and three during the nestling stage (two broods disappeared, and one brood was found pecked to death, but only one chick eaten).

Nest selection. Nests appeared to be selected more often by Amur Falcons as nest bowl percent cover ($F_{1,192} = 14.3$, $P < 0.001$) and distance to forest edge ($F_{1,192} = 6.0$, $P = 0.015$) increased, and these two parameters were included in all of the top five models (Table 2). Parameter estimates show that the effect of nest bowl cover

(0.077) was greater than the effect of distance to forest edge (0.053). The top model was nested within subsequent highly ranked models, none of which provided a significantly greater fit than the top model (all $P > 0.24$), so there is no evidence that additional parameters in subsequent models contribute to model performance. Active falcon nests had greater average percent cover of nest bowls than inactive nests (74% vs. 43%; $t_{32.94} = 5.2$, $P < 0.0001$) and tended to be farther (13 m vs. 6 m; $t_{22.12} = 1.9$, $P = 0.07$) from forest edges.

Spatial patterns in nest-site selection. Amur Falcons nested an average of 132 m (95% CI = 60–204 m) from the nearest active Eurasian Magpie nest, but this did not differ from the expected value of 158 m (95% CI = 90–225 m) estimated by our null simulation ($P = 0.61$). Amur Falcons nested an average of 203 m (95% CI = 148–257 m) from the nearest active Amur Falcon nest, although, in one case, two falcon nests were only 72 m apart, and one falcon nest was 446 m from the nearest conspecific nest. This average did not differ significantly from the expected value of 222 m (95% CI = 128–316 m) from our null simulation. Active Eurasian Magpie nests were 86 m (95% CI = –2 to 175 m) farther from each other than predicted by a random simulation using existing nest structures. We also discovered seven nests of other falcon species, including Eurasian Hobby (*Falco subbuteo*), Common Kestrel (*F. tinnunculus*), and Lesser Kestrel (*F. naumanni*; Table S2). We used the same simulation methods to tests whether Amur Falcons nested farther from these species than predicted by chance and found the observed average distance of 570 m did not

Table 1. Top-ranked nest survival models for Amur Falcon nests at Hustai National Park, Mongolia.

	Model ^a	Npar	AIC _c	DeltaAIC _c	Weight	Deviance
1	S(~ 1)	1	76.29	–	0.25	74.28
2	S(~ %Cover)	2	77.19	0.91	0.16	73.17
3	S(~ Date)	2	77.83	1.54	0.12	73.81
4	S(~ NestAge)	2	77.99	1.71	0.11	73.97
5	S(~ ForestEdge)	2	78.01	1.73	0.11	73.99
6	S(~ Stage)	2	78.03	1.74	0.10	74.00

^aModels were fit using the package “RMark” (Laake 2013). Covariates include nest age (time since nest initiation), date, nest stage (incubation vs. nestling), nest bowl percent cover, and distance to forest edge.

Table 2. Top five nest selection models for Amur Falcons at Hustai National Park, Mongolia, from “gl-multi” in R.

	Model ^a	npar	AIC _c	DeltaAIC _c	Weight	Deviance
1	AMFA ~ 1 + Cover + ForEd	3	85.412	–	0.093	16.929
2	AMFA ~ 1 + Cover + ForEd + Cond	4	86.029	0.617	0.068	16.809
3	AMFA ~ 1 + Cover + ForEd + Dia	4	86.118	0.706	0.065	16.816
4	AMFA ~ 1 + Cover + ForEd + Ht	4	86.401	0.989	0.057	16.841
5	AMFA ~ 1 + Cover + ForEd + TrEd	4	86.866	1.454	0.045	16.807

^aCovariates include nest bowl percent cover (Cover), distance to forest edge (ForEd), nest condition (Cond), nest diameter (Dia), and distance from edge of tree (TrEd). Multiple pairwise ANOVAs showed that none of these models (2–5) was a significant improvement over the top model.

differ from the expected null value of 585 m (95% CI = 411–759 m).

DISCUSSION

Amur Falcons in our study nested an average of 7 d earlier than those farther north in Mongolia (Schäfer 2003). It is difficult to know whether this difference is due simply to interannual variation. Incubation periods, clutch sizes, and density of Amur Falcon nests were similar between the studies. In northern Mongolia, however, most nests were in pine trees rather than birches (Schäfer 2003). In both studies, most falcons used Eurasian Magpie nests.

Nest survival. Mean DSR estimates provide a less biased metric for nest success and survival than apparent survival rates for most species (Brown et al. 2013). Our model selection approach did not detect effects of nest age, nest stage, initiation date, or nest-structure parameters on survival. Instead, our intercept-only model estimated a single DSR for all nests. Our small sample of nests ($N = 21$) likely limited our power to detect potentially significant effects for these covariates that have contributed to model performance in larger falcon datasets (Brown and Collopy 2008, Brown et al. 2013). Our apparent nest survival estimate of 60% of nests surviving to fledging is slightly lower than past apparent nest survival estimates for Amur Falcons of 73% (Schäfer 2003) and 89% (Usukhjargal et al. 2012), although a bit higher than Kotymán et al. (2015) found for Red-footed Falcons (49%). However, this apparent survival metric is often biased upwards (Brown et al. 2013) and not easily

comparable to our model-based approach where we estimate a non-biased DSR leading to an overall nest success estimate of 31.6%. This is lower than model-based estimates in similar studies for American Kestrels (60%) (Brown et al. 2013) and Lesser Kestrels (~ 55%) (Sarà et al. 2012). The summer of 2017 was a very dry year at HNP, which may have contributed to the low nest success.

Nest selection. Eurasian Magpies typically build a new nest each year, perhaps because the effort required to do so is minor compared with the physiological costs of producing eggs and the entire breeding effort (Stanley 2002). Magpie nests survive 2–4 yr and, at a site in China (Zhou et al. 2009), approximately half were either reused or usurped by birds of prey. We found that the falcons typically chose nests that were farther from forest edges and that provided greater cover over the nest bowl, usually in the form of a complete dome of sticks with multiple side entrances. Closed nests likely provide increased protection from predators; closed nests, natural cavities, and nest boxes are preferred and can increase nest survival of other small falcon species (Sumasgutner et al. 2014, Kotymán et al. 2015), although not always (Bobek et al. 2018). In contrast to our results, Zhou et al. (2009) found that magpie nests closer to forest edges were more likely to be reused by raptors. That study, however, was in an area that was largely forested whereas the patches of birch trees in our study area were relatively open, sparse, and small (maximum distance to an edge in our study area was ~ 75 m); most falcons we observed nested within 15 m of a forest edge. Falcons may prefer to be near the edges of

large forest patches for easier access to their more open foraging habitat (Zhou et al. 2009), but they appear to prefer being 10–15 m from edges (revealed in our study of small patches), possibly so nests are less visible to potential predators. As birch trees die in HNP and across the Mongolian steppe (Verhoeven et al. 2018), leading to a reduction in size of already small forest patches, fewer patches will be large enough to provide nest sites that far from forest edges.

Spatial patterns in nest-site selection. The spatial patterns of nests of Amur Falcons in our study did not differ significantly from random expectations. We found no evidence that they selected nests either farther from or closer to conspecifics or other members of the same genus than predicted by chance. Our null simulation considered both the location of potential nest structures and the preferences of falcons for certain nest characteristics and thus should have been a good test of spatial selection preferences.

This spatially random pattern contrasts with that of their colonial-nesting sister species, the Red-footed Falcon. Some of this difference between colonial-nesting Red-footed Falcons and solitary-nesting Amur Falcons may simply be due to the use of the nests of different species of corvids. The former often uses the nests of Rooks (Purger and Tepavčević 1999, Kotymán et al. 2015), which nest colonially. European Magpies, based on our simulations, preferentially nest farther from each other than predicted by chance. This difference in the nesting behavior of Eurasian Magpies and Rooks may contribute to the lack of coloniality in Amur Falcons, but our simulations show that Amur Falcons could have nested closer together than they did given the availability of suitable Eurasian Magpie nests, so it is unlikely that this difference alone explains solitary nesting by Amur Falcons.

Haraszthy and Bagyura (1993) purported to show that Red-footed Falcons had higher nesting success when nesting in colonies than when nesting solitarily. Colony nesting is thought to occur when the benefits of reduced predation and increased information transfer (due to the proximity of conspecifics) outweigh the costs of competition (Rolland et al. 1998, Evans et al. 2016), but this hypothesis is difficult to test. Cecere et al.

(2018) showed that neighboring colonies of Lesser Kestrel did have colony-specific foraging grounds, providing evidence for the importance of information sharing among individuals. If such information transfer is important for Amur Falcons in HNP, they may gain sufficient information from conspecifics by all nesting in the few wooded valleys available in our study area (see below).

Our simulations quantitatively confirm the general observation that Amur Falcons are not at either end of the solitary-colonial spectrum, but rather occupy an intermediate position. Amur Falcons do not actively exclude other pairs from the areas around their nests, as American Kestrels are known to do (Village 1983), because, in several cases, adjacent nests in our study were within a few meters of each other. However, neither do Amur Falcons actively seek to aggregate in colonies like Lesser Kestrels (Di Maggio et al. 2016, Cecere et al. 2018), even when magpie nests were sufficiently dense in our study area to permit it.

Although neither clustered nor overdispersed within our study area, on the scale of the entire Hustai National Park, nesting Amur Falcons were concentrated in the few wooded valleys where large numbers of magpie nests (and birch trees) were available. Competition for food is likely not a factor in preventing Amur Falcons from nesting in colonies because, when nesting in HNP at a density of 3.5 nests per km², adults likely still have foraging ranges that either largely overlap or that require some adults to forage far from nesting areas. The home range size of breeding Amur Falcons has not been quantified, but similar-sized Lesser Kestrels (*Falco naumanni*) typically have home ranges ranging in size from 25 to 45 km², with many overlapping feeding ranges around colonies (Vlachos et al. 2015, Gustin et al. 2017).

Just as Amur Falcons do not appear to consider the location of conspecifics when choosing nest sites, they also do not appear to consider the location of active Eurasian Magpie nests. This is surprising given that magpies are known nest predators of not only small passerines, but also partridges that are larger than Amur Falcons (Madden et al. 2015). Schäfer (2003, as cited by Stubbe et al. 2010) observed Amur Falcons chasing magpies from, and co-opting, their nests so

magpies may be loath to attack falcon nestlings. We observed no aggressive interactions between these species, but one of us (SG) did observe a Eurasian Magpie carrying the egg of a small falcon in its bill in 2010. Falcons may co-opt active magpie nests simply because they prefer the location or nest structure, but there is also evidence that newer magpie nests have fewer ectoparasites and are, therefore, more desirable for falcons (Prokop 2004, Zhou et al. 2009). Such co-option can have a larger impact than predation on magpie nest survival (Prokop 2004).

In summary, we provide the first model-based assessments of nest survival, nest-site selection, and spatial nesting patterns for Amur Falcons. Ongoing tree loss in Hustai National Park and across the Eurasian steppe likely represents a threat to the reproductive rates of this species. Additional studies of nesting Amur Falcons are needed to quantify the foraging ranges of adults, nestling diets, and fledgling survival as well as interannual site fidelity of both established adults and new recruits.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Appendix S1. R code for Amur Falcon (*Falco amurensis*) nest site selection simulation. This simulation code randomly distributes Amur Falcon nests among unoccupied Eurasian Magpie nest structures in the study area to compare the observed vs. predicted pattern of spatial distribution of Amur Falcon nests relative to each other.

Appendix S2. R code for Amur Falcon (*Falco amurensis*) nest site selection simulation. This simulation code randomly distributes Amur Falcon nests among unoccupied Eurasian Magpie nest structures in the study area to compare the observed vs. predicted pattern of spatial distribution of Amur Falcon nests with respect to Eurasian Magpie nests.

Table S1. Amur Falcon nests monitored in Hustai National Park, Mongolia, in 2017.

Table S2. Characteristics of current and former Eurasian Magpie nest structures monitored in Hustai National Park (HNP), Mongolia, in 2017.

Table S3. Average measurements (SD) of nestling Amur Falcons (*Falco amurensis*) from nests in Hustai National Park, Mongolia.

Table S4. Characteristics of former Eurasian Magpie nest structures used by Amur Falcons in Hustai National Park (HNP), Mongolia, in 2017.