Influence of nest box design on occupancy and breeding success of predatory birds utilizing artificial nests in the Mongolian steppe

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SUMMARY

We monitored 100 artificial nests of four different designs to examine the occupancy and breeding success of predatory birds in nest site limited, steppe habitat of central Mongolia. Three species, upland buzzard *Buteo hemilasius*, common raven *Corvus corax* and saker falcon *Falco cherrug*, occupied artificial nests in all years and their number increased over the five-year study period, when the number of breeding predatory birds rose from 0 to 64 pairs in our 324 km^2 study area. The number of breeding pairs of saker falcons increased at a faster rate than ravens, reflecting their social dominance. Saker falcons and common ravens preferred to breed inside closed-box artificial nests with a roof, whereas upland buzzards preferred open-top nests. For saker falcons nest survival was higher in closed nests than open nests but there was no significant difference in laying date, clutch size and brood size in relation to nest design. This study demonstrates that whilst nest boxes can increase breeding populations in nest site limited habitats, nest design may also influence occupancy rates and breeding productivity of the species utilizing them. Careful consideration is needed in designing nests to maximize occupancy rates and productivity.

BACKGROUND

In Mongolia, the globally endangered saker falcon *Falco cherrug* is harvested from the wild for the international falconry trade, yet little is known about the implications of this harvest for the conservation of the species (Dixon *et al*. 2011). The use of artificial nests is a well-established conservation technique (Jones 2004), which can be used to increase the size and distribution of breeding bird populations that are limited by the availability of natural nesting sites (Cade & Temple 1995). Saker falcons are known to utilize artificial nests (Dixon *et al.* 2013) and in nest site limited habitats there is the potential to create a managed and easily monitored population in artificial nests, which could potentially support a sustainable harvest (Rahman *et al.* 2014). Furthermore, artificial nests could contribute to the control of rodent pest species in the steppe ecosystem by increasing predator densities and predation rates (e.g. Meyrom *et al.* 2009, Paz *et al.* 2013).

In order to optimize the efficacy of using artificial nests to increase the breeding population of saker falcons and other predatory species we needed to identify nest designs that are (a) preferred by them and (b) maximized their breeding success. The suitability of an artificial nest depends on location and its capability to provide sufficient accessibility and space for breeding, as well as protection from predators and the environment (Lambrechts *et al.* 2012). The requirements of a nest will differ between species and an awareness of species-specific preferences could potentially allow for a more targeted approach to nest site supplementation. However, nest design is rarely considered in relation to occupancy and nesting success (Lambrechts *et al.* 2010, 2012).

Our study site was established in Darkhan district, Khentiy province, central Mongolia (Figure 1). In flat and undulating landscape the habitat was characterized by degraded steppe grassland with sparse, low vegetation cover. The study area was heavily grazed by livestock (mainly sheep, goats and horses) belonging to local nomadic herding families, who moved short distances (generally 5-10 km) between seasonal grazing areas. There were few raised substrates suitable for use by breeding raptors within the grid area. In this study we report on the occupancy of four different designs of artificial nest targeted at predatory birds (saker falcon, upland buzzard *Buteo hemilasius* and common raven *Corvus corax*) occupying nest site limited steppe habitat in central Mongolia. We further examined the influence of nest box design on nesting success and breeding productivity.

ACTION

Nest Design: In autumn 2005 we established a grid of artificial nests in our study area, which consisted of 100 artificial nests spaced at 2 km intervals in a 10 x 10 array covering an area of 324 km^2. Artificial nests were made from 60 cm diameter steel drums and comprised four different designs (N = 25 of each design) that were randomly distributed across the grid (Figure 1). Three nest box designs were open-topped: “shallow” (approximately 30 cm wall height), “deep” (approximately 60 cm wall height) and “sheltered” (approximately 30-60 cm wall that was higher on one side than the other) boxes, whilst the fourth design was a “closed box” 60 cm tall with a side entrance 30 cm high × 40 cm wide (Figure 2). The artificial nests were bolted on top of a 3 m steel pole that was fixed in the ground with concrete at depth of 0.5-0.6 m. Holes were punched in the base of each box for water drainage and the interior lined with a layer of fine gravel (approximately 5 cm deep).

Nest monitoring: During 2006-08, we monitored all artificial nests from early April to mid-July, visiting each nest an average of six times at 13 day intervals. Due to logistical constraints,

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ISSN 1758-2067

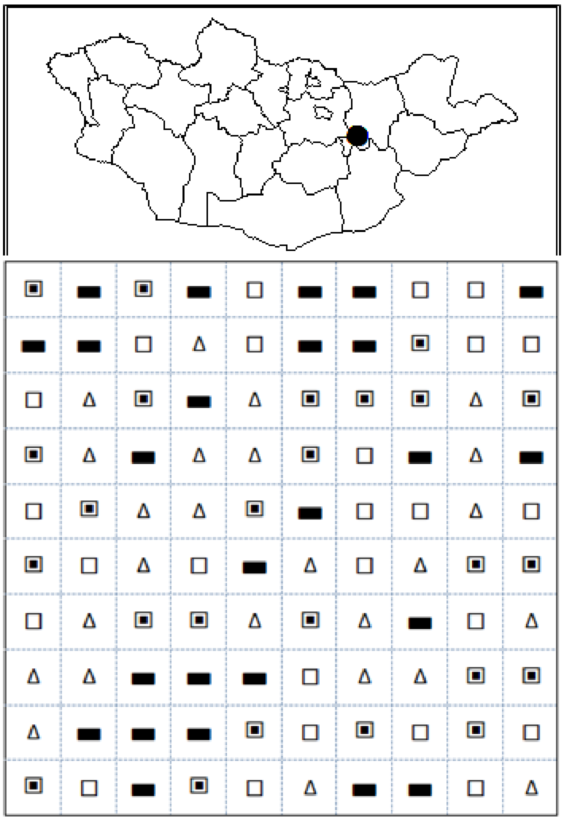

Figure 1. Location of study site, Khentiy province, Mongolia (top) and random distribution of artificial nest designs at the Darkhan grid (below, nests were erected at 2 km intervals), ▬ = shallow, □ = deep, Δ = sheltered, ▣ = closed box.

only one visit was made in 2009 (late April) and 2010 (late May) to check nests. The number of artificial nests standing each year reduced as some nests were removed by third parties and others fell down (Table 1). In determining breeding occupancy, we only considered nests where at least one egg was known to have been laid. We established a chronology for each nest, where the laying date of the first egg (FED) was estimated based on eggs in a clutch being laid daily for common raven, at two-day intervals for saker falcons and three-day intervals for upland buzzards. Apart from nests found during egg-laying, the FED was estimated by backdating from an estimated hatch date. For this backdating process we assumed that incubation covered 22, 35, and 37 days from the penultimate egg for common raven, saker falcon and upland buzzard respectively (Cramp & Simmons 1980). For saker falcons, chick age was estimated in the field by reference to a photographic chart illustrating growth development for a captive-bred chick at three-day intervals from 1 to 42 days old. For common raven and upland buzzard, chick development in the field was recorded using the coding of the British Trust for Ornithology 'Nest Record Scheme' (Ferguson-Lees *et al*. 2011), which was subsequently converted to an age range in days. The age ranges were derived from photographic guides for aging the nestlings of these two species compiled in 2009 (Y. Tadehara & A. Dixon, unpublished data). For common raven we used the following age ranges for each code: NA (naked) = 1-7 days old, IP (primaries in pin) = 8-13 days old, SP (short primaries) = 14-25 days old, MP (medium primaries) = 20-31 days old, LP (long primaries) = 32-37 days old and RF (ready to fledge) = 38-41 days old, whilst for upland buzzard codes were transformed to an age-range in the following way: DO (downy) = 1-9 days old, IP = 9-14 days old, SP = 15-25 days old, MP = 26-33 days old, LP = 34-43 days old and RF = 44-55 days old. We used the median value to obtain an estimate of hatch date after backdating from the age ranges obtained from each nest visit during the nestling stage. For nests that we were not able to estimate a FED using the above methodology, such as those that were first observed during incubation and failed before hatching, we used the mean FED for nests in the particular year.

Clutch size and brood size were recorded as the maximum number of eggs or chicks observed in a nest. Fledged brood size was recorded as the number of nestlings on the last monitoring visit, that were at least 30 days old or known to have fledged, for all three species. Observed nesting success was measured as the proportion of nests with known outcome that fledged at least one nestling.

Data Analysis: We used Analysis of Covariance (ANCOVA) to determine if there was any difference in the rate of breeding population increase among species over the five-year study period. To examine whether species differentially selected specific nest box designs for breeding, we used X^2 tests for each species separately. For each species, we used the Student's t-test to compare mean clutch and fledged brood sizes in closed and open nest boxes. All analyses were performed in R (R Development Core Team 2013).

We used MARK Version 5.1 (White and Burnham 1999, Dinsmore *et al.* 2002) to develop a number of candidate models where daily survival rate (DSR) was constant or varied temporally during the breeding season, with nest design (closed or open), nest age, stage of nesting period (incubation or nestling stage) and year as covariates. We used the Akaike information criterion (AIC_c) weights (w_i) to evaluate these candidate models. We calculated daily nest survival rate for each species from the weighted average of all candidate models that had a normalized AIC weight (w_i) > 0.01. The probability of overall nest survival was determined by raising the DSR to the power of 83, 66 and 93 for saker falcons, common ravens, upland buzzards respectively; these values being the median duration of the nesting period in days for each species respectively.

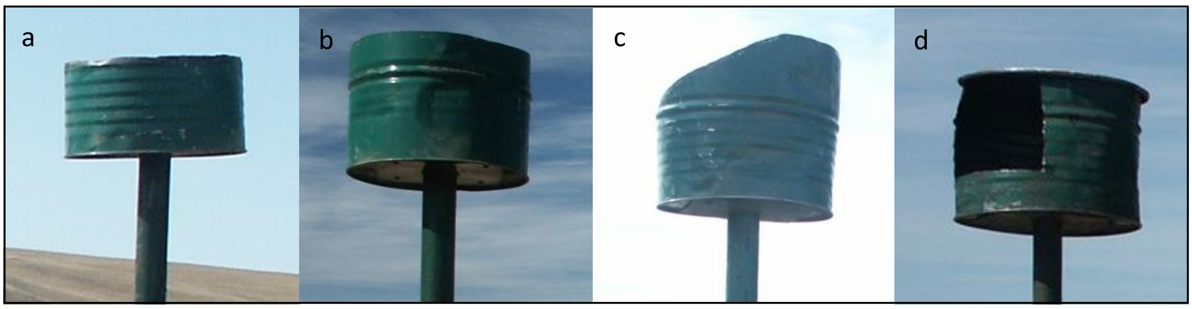

Figure 2. Different design of artificial nests: (a) shallow, (b) deep, (c) sheltered and (d) closed box.

ISSN 1758-2067

Table 1. Number of artificial nest sites in the study area occupied by different species in each year (% standing nests occupied).

	2006	2007	2008	2009	2010
Number of nests available	98	98	96	87	84
Golden eagle	0 (0.0)	1 (1.0)	0 (0.0)	0 (0.0)	0 (0.0)
Upland buzzard	11 (11.2)	17 (17.3)	14 (14.6)	18 (20.7)	30 (35.7)
Saker falcon	3 (3.1)	10 (10.2)	12 (12.5)	17 (19.5)	21 (25.0)
Common kestrel	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (1.2)
Common raven	5 (5.1)	6 (6.1)	9 (9.4)	10 (11.5)	12 (14.3)
Total	19 (19.4)	34 (34.7)	35 (36.5)	46 (51.7)	64 (76.2)

CONSEQUENCES

Occupancy: Over the period of 2006-10, five different species bred at the artificial nests, though common kestrel *Falco tinnunculus* and golden eagle *Aquila chrysaetos* only nested on single occasions. The most frequent breeding species was upland buzzard with 90 nests initiated, followed by saker falcon with 63 and common raven with 42 (Table 1). The number of breeding pairs of all three species increased over the five-year period with saker falcons increasing at a significantly higher rate than common ravens (effect of year: $F_{(1, 6)} = 307.2$, $p < 0.001$; effect of year x species: $F_{(1, 6)} = 58.8$, $p < 0.001$; Figure 3).

Nest design selection: Saker falcons ($\chi^2 = 51.32$, 1 d.f., $p < 0.001$) and common ravens ($\chi^2 = 20.65$, 1 d.f., $p < 0.001$) selected closed nest boxes most frequently. Although the proportion of breeding pairs of both species occupying open boxes increased over the study period, the preference for closed nest boxes was exhibited by saker falcons in each year, but this was not the case for common raven when no preference was

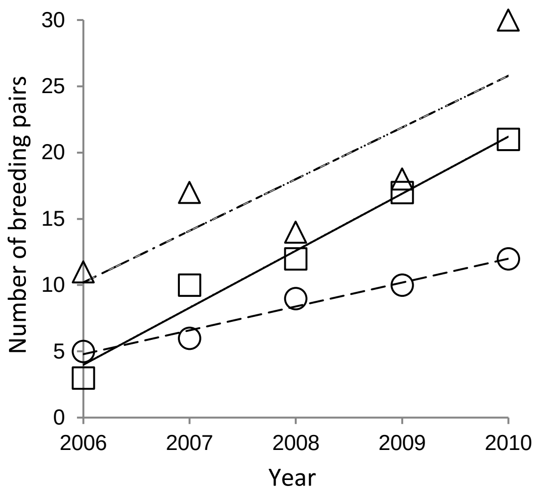

Figure 3. Number of breeding pairs of saker falcon, common raven and upland buzzard at the grid of artificial nests over the period 2006-10. Linear regression illustrates rate of population increase for each species. □ = saker falcon (solid trend line), ○ = common raven (dashed trend line), Δ= upland buzzard (dot-dash trend line).

Table 2. Percentage of saker falcons and common ravens occupying closed boxes, together with χ^2 tests in relation to their availability in different years. Number in parentheses is total number of artificial nests occupied each year.

Year	Saker falcon		Common raven	
	% (n)	χ^2 (p)	% (n)	χ^2 (p)
2006	67 (3)	2.91 (<0.05)	60 (5)	1.85 (0.09)
2007	70 (10)	9.88 (<0.01)	83 (6)	7.96 (<0.05)
2008	75 (12)	15.36 (<0.01)	67 (9)	6.90 (<0.05)
2009	47 (17)	4.60 (<0.05)	40 (10)	0.76 (0.38)
2010	48 (21)	7.08 (<0.01)	33 (12)	0.30 (0.45)

exhibited in 2009 and 2010 (Table 2). We found no significant difference in the use of shallow, sheltered or deep open box designs by saker falcons ($\chi^2 = 0.71$, 2 d.f., $p = 0.70$) and common ravens ($\chi^2 = 0.19$, 2 d.f., $p = 0.91$). In contrast, upland buzzards selected open boxes for nesting ($\chi^2 = 18.3$, 1 d.f., $p <0.001$). Among the open nest boxes, upland buzzards selected mainly deep open boxes ($\chi^2 =16.5$, 2 d.f., $p <0.001$).

Nest survival and breeding success: Saker falcon: for nests with known outcome, the observed nesting success was higher in closed boxes (0.83, n = 12) compared to open boxes (0.17, n = 6). The most parsimonious model to explain nest survival incorporated the additive effects of nest design and year (Table 3). We found no evidence that DSR varied with nest age or at different stages of the nesting period. Daily nest survival was higher in closed nest boxes compared to open nest boxes, with 71% of closed nests successfully producing fledglings compared to 23% of open nests (Table 4). There was no significant difference between closed and open boxes in relation to mean clutch size ($t = 0.02$, 36.1 d.f., $p = 0.98$) and brood size ($t = 0.14$, 19.5 d.f., $p = 0.88$) (Table 4). Overall, the mean fledged brood size at successful nests was 3.6 fledglings (n = 5).

Common raven: observed nesting success was higher in closed boxes (0.90, n = 10) compared to open boxes (0.60, n = 5). All the models we evaluated to explain nest survival were equally parsimonious (Table 3), despite overall nest survival being higher in closed nest boxes compared to open nest boxes (Table 4). There was no significant difference between closed and open boxes in relation to mean clutch size ($t = -0.05$, 5.0 d.f., $p = 0.96$) and mean brood size ($t = -1.45$, 31.2 d.f., $p = 0.15$) (Table 4). Overall, common ravens produced 3.0 fledglings per successful nest (n = 7).

Upland buzzard: with one exception, all upland buzzard nests were in open boxes, so nest design was not included in the nest survival model. Observed nesting success was 0.37 (n = 32). The most parsimonious model to explain nest survival incorporated year as a covariate (Table 3) and overall an estimated 42% of nests successfully produced fledged young (Table 3). Upland buzzards produced 1.3 fledglings per successful nest (n = 10).

DISCUSSION

Although upland buzzards can frequently (and saker falcons rarely) nest on the ground in the Mongolian steppe (Ellis *et al.* 1997, Gombobaatar *et al.* 2010), there were no known nests of either species in the area where we erected the artificial nest grid, yet by the end of the study in 2010 there were 64 pairs of predatory birds breeding in the 324 km^2 area of the artificial nest grid. This study clearly demonstrates that by providing artificial

ISSN 1758-2067

Table 3. Daily nest survival models for saker falcon, common raven and upland buzzard. All models feature intercept-only constant survival S (.). Models are ranked by ascending ΔAIC_c with a difference <2 indicating equal fit; w_i is the normalized AIC weight and K is the number of parameters.

Species	Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Saker falcon (n = 18 closed, 7 open)	S (.) $_{Design + Year}$	31.89	0.00	0.97	3	25.87
	S (.) $_{Design}$	39.74	7.85	0.02	2	35.73
	S (.) $_{Design + Stage}$	41.61	9.72	0.01	3	35.59
	S (.) $_{Year}$	43.85	11.96	0.00	2	39.84
	S (.)	46.70	14.81	0.00	1	44.70
	S (.) $_{Nest Age}$	48.56	16.67	0.00	2	44.55
	S (.) $_{Stage}$	48.70	16.81	0.00	2	44.69
Common raven (n = 14 closed, 6 open)	S (.) $_{Design}$	23.91	0.00	0.25	2	19.89
	S (.)	24.01	0.09	0.23	1	22.00
	S (.) $_{Design + Stage}$	25.30	1.39	0.12	3	19.27
	S (.) $_{Stage}$	25.61	1.70	0.11	2	21.59
	S (.) $_{Design + Year}$	25.66	1.75	0.10	3	19.63
	S (.) $_{Year}$	25.80	1.89	0.10	2	21.78
	S (.) $_{Nest Age}$	25.84	1.93	0.09	2	21.82
Upland buzzard (n = 40 open)	S (.) $_{Year}$	102.26	0.00	0.83	2	98.25
	S (.)	106.67	4.41	0.09	1	104.66
	S (.) $_{Stage}$	108.37	6.11	0.04	2	104.36
	S (.) $_{Nest Age}$	108.65	6.40	0.03	2	104.65

nest sites it is possible to increase the breeding population of raptors in nest site limited areas. Previous studies have also reported that the breeding populations of target species can be increased through providing artificial nests e.g. common kestrel (Fargallo *et al.* 2001) and barn owl *Tyto alba* (Meyrom *et al.* 2009).

Breeding recruits could be novel breeders drawn from a non-breeding population; alternatively they could colonise the artificial nests by breeding dispersal from pre-existing nesting sites elsewhere. During our five-year study the breeding population of three species increased, indicating that the annual number of potential breeding recruits for each species was limited; if this was not the case the maximum number of pairs could potentially have bred in the first year of our study. This suggests that most breeding colonists at the artificial nests were derived from a finite source, most likely the local non-breeding population. Alternatively, breeding recruits may be pre-existing breeders that gradually disperse to the grid in limited numbers each year, once they became aware of the artificial nests. However, saker falcon and raven territories exhibit a high degree of constancy across years (Ratcliffe 1997, Rahman *et al*. 2014), and such site fidelity suggests that breeding dispersal is limited in these species. The rate of population increase was highest for the saker falcon, perhaps reflecting the interspecific dominance of this species over the upland buzzard and common raven; saker falcons are able to usurp the active nests of both species and consequently they can limit the number of pairs of these species occupying the same grid.

Saker falcons exhibited a preference for closed boxes compared to open boxes, as did common ravens. However, as saker falcon and common raven breeding numbers increased, eventually surpassing the number of available closed boxes, both species utilized open boxes; common ravens to a greater extent, presumably because saker falcons were dominant competitors for the closed box nest sites. In the later years of our study the preference for closed boxes previously exhibited by common ravens was not evident, reflecting the fact that in these years most closed boxes were occupied by the dominant saker falcons.

Whilst the internal space of the closed nests may have been too small to accommodate the large upland buzzards, we believe that their avoidance of nesting inside closed boxes was not primarily due to the size of the box. Nest design preference is likely to be influenced by phylogeny as much as ecology, with several species of falcon and corvid being regular cavity nesters, whereas no buzzard species are cavity nesters (del Hoyo *et al.*

Table 4. Breeding parameters for saker falcon, common raven and upland buzzard occupying closed and open artificial nests. FED = date of first egg laid ± S.E. (n), c/N = mean clutch size ± S.E. (n), b/N = mean brood size ± S.E. (n), DSR = daily nest survival rate (95% confidence limits; n) and Nest Survival = % of nests surviving whole nesting period (95% confidence limits; n).

Design	Saker falcon		Common raven		Upland buzzard
	Closed	Open	Closed	Open	Open
FED	05 April ± 7 days (28)	03 April ± 10 days (12)	24 March ± 2 days (13)	22 March ± 2 days (3)	21 April ± 2 days (18)
c/N	3.8 ±0.8 (24)	3.8 ±0.9 (18)	4.7 ±0.3 (7)	4.8 ±0.5 (4)	3.0 ±0.1 (67)
b/N	3.7 ±0.7 (28)	3.6 ±1.1 (11)	3.7 ±0.2 (20)	4.1 ±0.2 (17)	2.6 ±0.1 (44)
DSR	0.996 (0.983-1; 18)	0.982 (0.948-0.994; 7)	0.997 (0.993-1; 14)	0.994 (0.982-1; 6)	0.991 (0.985-0.996; 40)
Nest Survival	71% (24-100%; 18)	23% (1-61%; 7)	84% (62-100%; 18)	67% (30-100%; 18)	42% (24-73%; 40)

ISSN 1758-2067

1994). The selection exhibited by upland buzzards for deep open boxes compared to shallow or sheltered open boxes was surprising, especially considering that the birds filled all boxes to the brim with nest material, which eliminated any variation in the amount of shelter provided to the nest cup by the different designs. The deeper boxes may have had an attraction for upland buzzards in that they were taller and more prominent than the other two designs.

Closed nest boxes provide more shelter from the weather, especially strong wind, for the eggs, chicks and incubating/brooding adult than open boxes. Saker falcons and common ravens breed earlier in the year than upland buzzards and consequently they are likely to face harsher weather than upland buzzards, and thus the extra shelter afforded by closed nests may be particularly important to these species. We have no evidence that open and closed nest boxes offered differential degrees of protection from potential predators as there was no direct evidence of predation at our nests during the study. We therefore do not think predator avoidance was an important factor influencing nest design choice in the saker falcon, common raven and upland buzzard.

A review by Lambrechts *et al*. (2012) reported that nest box design can potentially affect breeding productivity by influencing the number and survival of eggs and chicks, their developmental rates and the physical condition of adults. Saker falcons and, to a lesser degree, common ravens breeding in closed boxes had a higher nesting success than their congeners utilizing open nests, and both species had better nesting success than upland buzzards that primarily used open nests for breeding. In spring the Mongolian steppe is characterized by frequent strong winds, often carrying sand or snow, and it is likely that closed boxes afforded greater protection for eggs, chicks and brooding adults in such weather conditions. Elsewhere in the central Mongolian steppe, we reported that nest survival of saker falcons in closed boxes was higher than that found in natural nests (Rahman *et al*. 2014), where the natural nests were typically ‘open’ sites, located in nests built by common ravens and upland buzzards on rock faces with varying degrees of shelter.

In conclusion, nest designs that include a closed box with an open tray on the roof are likely to maximize the chances of occupancy by predatory birds in the Mongolian steppe, because they provide suitable nesting situations for both species that prefer closed nests (saker falcon and common raven) and those that prefer open nests (upland buzzard).

ACKNOWLEDGEMENTS

This study was funded by and conducted on behalf of the Environment Agency-Abu Dhabi (EAD). We thank the following who helped collect data in the field: S. Gombobaatar, B. Odkhuu, B. Munkhzaya, S. Amarsaikhan, M. Etheridge, S. MacPherson, M. Jessen, O. Milenkaya, B. Grubac, P. Andreano, G. Papp, and N. Nedyalkov.

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