Causes of population declines of the Lesser Kestrel *Falco naumanni* in Israel

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We studied the ecology of the Lesser Kestrel *Falco naumanni*, a globally threatened species, to identify the factors causing its gradual decline in Israel, in order to stabilize and possibly restore its numbers. Lesser Kestrels in Israel breed in colonies, both adjacent to human settlements (rural and urban) and in the countryside, where they are found especially on cliffs. In this study, observations of Lesser Kestrels were carried out in three different breeding areas: (1) an urban colony in Jerusalem, (2) a rural colony in the Alona district and (3) a cliff in the Judean desert (open landscape colony) about 10 km east of Jerusalem. The number of fledglings per nest in Jerusalem (1.91) was lower than in Alona (2.44) and the cliff (3.16). As this lower productivity was associated neither with the clutch size, with hatching success, which were similar in all three regions (about four eggs per clutch, and 80% hatched, respectively), nor with egg fertility, it probably reflects factors operating during the nestling phase. We suggest that the two main factors limiting food availability and causing nestling deaths in Jerusalem are the relatively long flight distances between the breeding and hunting sites, and the use of pesticides in the city parks and lawns. Stochastic events superimposed on such factors, such as the drought of 1999, which markedly reduced productivity, may cause pronounced fluctuations eventually affecting long-term population persistence.

The Lesser Kestrel *Falco naumanni* is a globally threatened species (BirdLife International 2000). Although there are no precise data on Lesser Kestrel global population size in the past, there is evidence that numbers fluctuated throughout its range between the years 1850 and 1955 (Siegfried & Skead 1971). Recently, many Lesser Kestrel colonies have been abandoned, and this has been associated with a dramatic decline in the world population. In the last 40 years, large population declines have occurred in most of the countries in which the Lesser Kestrel breeds (Negro 1997). As a result, the western European population has declined by 95% since 1950, and the South African wintering population has declined by 50% since 1971 (BirdLife International 2000). The world Lesser Kestrel population has decreased by more than 20% in the last 10 years and it is therefore now listed as globally endangered and vulnerable by the IUCN (Evans 1994).

Several suggestions have been made to explain these population declines. Cramp and Simmons's (1980) suggestion that secondary poisoning due to the use of pesticides in agriculture and heavy metals in industry might be a cause was rejected by Negro et al. (1993); and Pomarol’s (1996) suggestion that a lack of nesting sites might be important was rejected by Forero et al. (1996). The true main cause for the reduction appears to be food shortage resulting from the intensification of agriculture and urban sprawl (Biber 1990). This has led to the decreasing availability of natural or extensively managed open areas, which are used by the Lesser Kestrel as foraging grounds (Donazar et al. 1993).

The Lesser Kestrel population has also declined in Israel. Up to the mid 20th century this bird was a very common summer breeder in Israel (Tristram 1865, Meinertzhagen 1925, Luke & Roach 1934). Later estimates suggest a total of 2000–3000 breeding pairs (Mendelssohn 1972) and about 10 000 pairs (Mendelssohn in Leshem 1979). All sources describe several major colonies, each hosting several hundred pairs up to the mid 20th century (Shirihai 1996). The number of breeding pairs has decreased during
the last 40 years, and today only 550 pairs still breed in Israel (Israel Ornithological Center Breeding Survey 2000).

Israel’s Lesser Kestrel populations are migratory. The birds winter in Africa and settle on their breeding colonies in February or March. The nests are located on cliffs and quarries, and in human settlements in niches and cavities in walls of old buildings or under roof tiles. Eggs (usually 3–5 per clutch) are laid in April and the young fledge in June or July. Both parents incubate the eggs for 1 month. The birds forage communally in open areas such as semideserts, grassland, pastures, tilled land and urban parks, and feed predominantly on insects and other invertebrates. They abandon the colonies between the end of June and mid July, when they begin to migrate south to their wintering grounds.

Following Tella et al. (1996), we hypothesize that the breeding performance of urban Lesser Kestrel populations is poorer than that in rural and natural habitats. There are many conflicts between the needs of Lesser Kestrel conservation and of human activity. Such conflicts exist in rural environments as a result of changes in agricultural practices (Tella et al. 1998) and in urban environments as a result of urban expansion (Tella et al. 1996). Our aim was to study the ecology of the Lesser Kestrel in colonies in urban, rural and natural areas (mainly cliffs) in order to determine which factors were likely to cause its population decline in Israel, especially in urban areas. Understanding these factors may assist in halting and possibly reversing the decline.

**METHODS**

**Study area**

The study was carried out in Israel between February and July in 1998 and 1999, and productivity was also measured in 2000 and 2001.

We monitored three Lesser Kestrel colonies (Fig. 1). The main study took place at an urban colony in the city of Jerusalem (31°45′N, 35°10′E, human population 630 000; area 126.5 km²). Here, Lesser Kestrels breed under the roofs of old houses, or in small cavities in the walls. They breed in small subcolonies ranging from two to 27 pairs, with a total of 60–80 breeding pairs. They forage mainly in the semi-arid area east of Jerusalem (Judean desert) and on small lawns and gardens inside the city.

The second study site was a rural Lesser Kestrel colony in the Alona area (32°35′N, 35°05′E), south of Mt Carmel, which comprises three settlements – Amikam, Aviel and Giv’at Nili. Approximately 100 pairs of Lesser Kestrels breed in old buildings. The area is characterized by hilly pasture and agricultural areas, offering suitable foraging sites.

The third study site was a Lesser Kestrel colony situated on a cliff in the Judean desert (31°30′N, 35°20′E) (away from human settlements) in an open, semidesert area. The cliff is located on the Jerusalem–Jericho road and approximately 15 pairs breed in small holes and cavities on the cliffs. There are two settlements nearby: Nofey Prat and Kfar Edomim. The Lesser Kestrels use the power lines around the settlements as sit-and-wait foraging perches.

**Productivity**

Productivity was estimated in all three colonies as the number of nestlings that reached 25 days of age (from hatching) per breeding attempt. Total failures (i.e. no nestlings fledged) were excluded from the productivity calculations because the number of fledglings in Alona and the Judean desert...
Population declines of the Lesser Kestrel was only counted in successful nests. Total failures were included only in order to calculate the proportion of successful pairs in Jerusalem. The nests in Jerusalem, Alona and the Judean desert were checked weekly during 1998 and 1999, until the nestlings had reached the age of 25 days (in 1999 the nests in the Judean desert colony were only checked for eggs because of later human disturbance in the area). At each nest we counted the number of eggs laid and hatched and the number of fledglings. If the exact number was not known, the minimum number possible was used for the analysis.

The terminology used in this paper on productivity is based on Steenhof (1987) for raptors in which a breeding pair is one that laid eggs, a successful pair is one that successfully raised at least one chick to fledging age and breeding success is the percentage of breeding attempts that were successful.

**Prey delivery rates**

Prey delivery rates to the nestlings were measured as the number of food items brought to the nest during a 6-h observation period. Observations took place in Jerusalem (nine nests) and Alona (four nests) during 1999. Every nest was observed for 6 h once a week, over a period of 4 weeks from hatching. Each observation period consisted of three 2-h observations, in the morning, noon and afternoon, in order to avoid differences in prey delivery rates during the day. The total observation period was 312 h on the nests (24 h on each nest).

**Distance between breeding and foraging areas**

The distance between the breeding and foraging sites of the Jerusalem Lesser Kestrel population was measured in two ways: by observations of ringed individuals at both their breeding and their hunting sites in 1998 and 1999; and by radiotelemetry in 1999. Until 1998, 187 Lesser Kestrels had been ringed with colour rings in Jerusalem. During this research another 185 birds were ringed with numbered plastic colour rings, which could be read with a telescope from a distance. In 1999 we used seven tail-mounted radio-transmitters. The tail mounts were attached to the two central tail feathers and did not seem to affect behaviour, breeding success or survival (see also Hiraldo et al. 1994). Four birds were captured in March outside Jerusalem and the other three birds were caught in April inside the city of Jerusalem. Two of the birds caught outside the city were also found to breed outside on a cliff, whereas the other two bred inside Jerusalem. Because one of the transmitters on a Jerusalem bird was damaged, it was only possible to track one of the birds captured outside the city later in the season. The three birds captured in April while foraging in the city were located in their Jerusalem nesting areas, but they did not breed that year. Therefore, except for one bird, the radiotagged birds provided little information. The birds were tracked once a week through May and June (nestling stage) in order to locate their breeding sites and to observe whether there were any changes in their hunting sites.

**Nestling growth rates**

In 1999, ten nestlings from Jerusalem (five nests) and ten from Alona (four nests) were weighed in the nest, once weekly (to the nearest 0.5 g; total of four weighings per season), and their wing length was measured to the nearest millimetre, in order to determine their growth rates and to compare them to 13 nestlings (three nests) that were raised in captivity in the Zoological Garden of Tel Aviv University, where food was supplied *ad libitum*. The nestlings were individually marked with animal markers (red, green and purple animal marking crayon).

**RESULTS**

**Productivity**

Data on average clutch size, hatching rate and number of fledged young during 1998 in the three colonies are shown in Table 1 and Figure 2. Clutch size did not differ between the three areas (one-way ANOVA,

<table>
<thead>
<tr>
<th></th>
<th>Hatching successa (%)</th>
<th>Fledging successb (%)</th>
<th>No. nestlings/successful pair ± sd</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jerusalem</td>
<td>68–90%</td>
<td>46–58%</td>
<td>1.91 ± 0.68</td>
</tr>
<tr>
<td>Alona</td>
<td>79–83%</td>
<td>52–62%</td>
<td>2.44 ± 1.42</td>
</tr>
<tr>
<td>Judean desert</td>
<td>80–88%</td>
<td>76–80%</td>
<td>3.16 ± 0.75</td>
</tr>
</tbody>
</table>

*aPercentage of eggs that hatched. bPercentage of eggs that produced a fledgling (age of 25 days).
F₂,23 = 1.486, P = 0.242), nor did hatching success (one-way ANOVA, F₂,23 = 0.779, P = 0.47). The only significant difference between the three areas was found in the mean number of fledged young per successful pair (one-way ANOVA, F₂,34 = 5.743, P = 0.007). A post hoc test revealed that productivity in Jerusalem was lower than in the Judean desert (Tukey's method, P = 0.05).

In 1999 there was a severe drought in Israel. Rainfall in Jerusalem and Alona was only 38% and 52% of the long-term average, respectively. In addition, there was also severe human disturbance at the nests in the Judean desert colony. These factors prevented us from combining the data from the two years or performing a multivariate analysis. In 1999 only 1.29 nestlings per successful pair fledged in Jerusalem (n = 31, sd = ±0.53). This does not include the 48 pairs (more than half of the population) that began to nest that year, but managed to fledge no nestlings at all. In Alona 1.67 nestlings per successful pair fledged (n = 3, sd = ±1.15).

\[ F_{2,31} = 1.486, \quad P = 0.242; \quad \text{hatching: } F_{2,23} = 0.779, \quad P = 0.47; \quad \text{fledging number: } F_{2,34} = 5.743, \quad P = 0.007. \]

In order to control for the effect of the number of nestlings in the nest on the amount of food brought to the nest, prey delivery rates were divided by the number of nestlings (Fig. 3). The results were the same: the amount of prey brought to the nest was influenced by nestling age (repeated measures ANOVA, F₁,7 = 8.418, P = 0.023**; n = 9 nests).

### Prey delivery rates

The nest provisioning rate increased through the nestling period in both Jerusalem and Alona (repeated measures ANOVA, F₂,14 = 15.706, P < 0.001, Table 2), and was higher in Alona than in Jerusalem (repeated measures ANOVA, F₁,7 = 35.621, P = 0.001, Table 2).

In order to control for the effect of the number of nestlings in the nest on the amount of food brought to the nest, prey delivery rates were divided by the number of nestlings (Fig. 3). The results were the same: the amount of prey brought to the nest was influenced by nestling age (repeated measures ANOVA, F₂,14 = 12.831, P = 0.001); and in Alona, prey delivery rates were higher than in Jerusalem (repeated measures ANOVA, F₁,7 = 8.418, P = 0.023).

An ANCOVA for feeding rates per nestling, with the study site as the nominal variant and the prey delivery rate as the dependent variable, revealed significant differences in feeding rates between

### Table 2. Average (± sd) number of prey items delivered to nestlings (1–3 weeks old) by male and female Lesser Kestrels, during a 6-h observation period, in Jerusalem (n = 6 nests) and Alona (n = 3 nests).

<table>
<thead>
<tr>
<th>Area</th>
<th>First week after hatching</th>
<th>Second week after hatching</th>
<th>Third week after hatching</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Prey Items(^a)</td>
<td>sd</td>
<td>Prey Items</td>
</tr>
<tr>
<td>Jerusalem</td>
<td>6.2</td>
<td>2.3</td>
<td>11</td>
</tr>
<tr>
<td>Alona</td>
<td>11</td>
<td>1.7</td>
<td>20.3</td>
</tr>
</tbody>
</table>

\(^a\)Number of prey items delivered in 6 h.
Jerusalem and Alona for females ($P = 0.0248$) and for the total ($P = 0.0113$), but was only close to significance for males ($P = 0.0594$). Nestling age was not shown to affect the feeding rates ($P = 0.45$), probably because of the small sample size.

**Distance between breeding and foraging areas**

Observations of ringed and radiotagged birds in Jerusalem in 1998 and 1999 showed that in February–April birds from Jerusalem forage mainly in the semi-arid areas east of the city, at a distance of 11.5–13 km from their nests. Two of the radiotagged birds that were later found nesting in Jerusalem were caught in the same area in March. In May and June (nestling stage) the flight distance between nesting and foraging sites of some of the ringed birds was 0.7–2.25 km (average distance 1.33 km, $sd = \pm 0.55$, $n = 6$). A radiotagged bird that was observed hunting 12 km from Jerusalem in March was also tracked hunting in the city 2.25 km from its nest in May. Observations on individually marked birds revealed that at least part of the Jerusalem breeding population foraged in the city during the nestling stage. On average it took the city foragers 8.2 min to fly the distance of 4.5 km from the foraging sites within Jerusalem to the nest and back to the foraging site ($n = 37$, $sd = \pm 1.42$).

**Nestling growth rates**

Figure 4 presents the nestling growth rates (g/day) of birds in Jerusalem, Alona and in captivity. Growth rates differed significantly across the three ‘treatments’ (repeated measures ANCOVA, covariate = age, $F_{2,28} = 40.433$, $P < 0.001$). A post hoc test revealed that the growth rates of nestlings in Jerusalem were significantly lower than those in either Alona or in captivity (Tukey’s method, $P = 0.05$). The three groups also differed significantly in the growth rates of nestling wing length (repeated measures ANCOVA, covariate = age, $F_{2,28} = 33.017$, $P << 0.001$).

**DISCUSSION**

The breeding Lesser Kestrel population of Israel has declined drastically in the last 40 years, from a few thousand (Mendelssohn 1972) to only 550 breeding pairs (Israel Ornithological Center Breeding Survey 2000). Many Lesser Kestrel colonies (e.g. Rosh Hanikra, Mt Arbel) have disappeared, and those that still exist have declined in numbers. The Jerusalem colony alone showed a 30% decline from 1997 to 2000 (Israel Ornithological Center Breeding Survey 2000; Table 3). Long-term data are needed in order to determine whether the decline in Jerusalem represents an actual trend, or whether it is part of a normal population fluctuation. Nonetheless, we cannot ignore the sharp decrease in the last 4 years. Interestingly, in our study, productivity was highest in a population breeding in a ‘natural’ type of environment, intermediate in a cultivated area and lowest in an urban area, suggesting a progressive decline in breeding performance along a gradient of increasing human activity. Such gradients are also likely to be common in other raptor species. However, the response to environmental alteration and degree of development is probably species-specific, some species declining along the gradient (e.g. this study, Tella et al. 1996), others increasing (e.g. Marchesi et al. 2002) and others being relatively unaffected (e.g. Sergio & Bogliani 1999).

It is possible that the decrease in the Jerusalem population has been caused by low productivity, because productivity was found to be much lower here than in either the Alona or the Judean desert colonies. Similar differences in productivity between

### Table 3. Number of Lesser Kestrel breeding pairs, successful pairs and proportion of successful pairs in Jerusalem in 1997–2001.

<table>
<thead>
<tr>
<th>Year</th>
<th>1997</th>
<th>1998</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeding pairs</td>
<td>86</td>
<td>88</td>
<td>82</td>
<td>62</td>
<td>53</td>
</tr>
<tr>
<td>Successful pairs</td>
<td>85</td>
<td>71</td>
<td>35</td>
<td>58</td>
<td>37</td>
</tr>
<tr>
<td>Proportion of successful pairs</td>
<td>99%</td>
<td>81%</td>
<td>43%</td>
<td>90%</td>
<td>70%</td>
</tr>
</tbody>
</table>

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Lesser Kestrels breeding in urban and rural settings have also been found in Spain (Tella et al. 1996). In the province of Seville (urban habitat) productivity was 2.2 nestlings/nest, whereas in Monegros (rural area) it was 3.7 nestlings/nest. Tella et al. (1996) showed that the main reason for the low productivity in urban areas was nestling starvation rather than nestling or egg predation, which are higher in rural than in urban areas.

Our data support the Spanish findings: in Jerusalem, the main cause of low productivity appears to be lack of food. We found no difference in clutch size between the three areas and the clutch size was similar to that found in other parts of the world range (Bijlsma et al. 1988, Negro et al. 1993, Tella et al. 1996, Il’yukh 1998). No differences were found in the hatching rates between our three study areas, and the hatching rates we measured (around 80%) in Israel were also similar to those reported from Spain (Negro et al. 1993). This is considered to be a high hatching rate in comparison with other raptors of the same size, such as the Sparrowhawk Accipiter nisus with a hatching rate of 60% (Newton 1986) and the Common Kestrel Falco tinnunculus with a rate of 64% (Village 1990). Therefore, the low productivity is related to factors occurring not at the egg stage but at the nestling stage. The significant difference in prey delivery rates between Jerusalem and Alona suggested that the low productivity in Jerusalem was associated with lack of food. In Jerusalem the birds managed to bring only one prey item to the nest per hour when the nestlings were 1 week old and 1.7 prey items per hour when the nestlings were 3 weeks old. In comparison, the birds in Alona brought 1.8 and 4.8 prey items when the nestlings were 1 and 3 weeks old, respectively.

One of the main reasons for lack of food in Jerusalem was probably the distance between breeding and foraging areas. Before the eggs hatched, the Lesser Kestrels foraged outside the city in open semi-arid areas, some 13 km from the breeding sites. The birds could be seen foraging in these areas until May, when the chicks hatched. Thereafter, they started to forage over the small grassy areas inside the city, which are located much closer to the breeding sites, at a maximum distance of 2.25 km. We suggest that because of the limited food availability in the city, the birds prefer to feed in the desert. However, during the nestling stage, when it becomes energetically too costly to make the long trip to the desert, the birds are forced to feed in the city. Those breeding in the agricultural settlement of Alona or on cliffs in the desert have large areas of open grassland available near the breeding areas, so food is less of a limiting factor there. It took the Lesser Kestrels 8 min to fly a distance of 4.5 km. Thus, the time it would take to fly from the breeding sites to the foraging areas in the semidesert (around 20 km) is approximately half an hour, excluding the time taken to capture the prey. Telemetry data collected by M. Frankel (pers. comm.) support this conclusion. She found that the home range size of Lesser Kestrels from the Jerusalem population was around 30 km² whereas that of an even larger natural colony was 7 km² (Kolmogorov–Smirnov two-sample test, $P = 0.006$).

The use of pesticides in Jerusalem gardens may further affect the local Lesser Kestrel population, which depends primarily on mole-crickets Gryllotalpa gryllotalpa. Gancz et al. (2000) examined the influence of Diazinon (a pesticide used to eliminate mole-crickets and which affects the enzyme acetylcholine esterase [AcheE] in birds and mammals) on Lesser Kestrels that feed on mole-crickets in Jerusalem. They found that immediately after the use of Diazinon AcheE, activity decreased by 43% in adults that had fed on the poisoned mole-crickets in comparison with other adult Lesser Kestrels ($P = 0.007$). The loss of hunting grounds as a result of the rapid pace of development of the city where the Lesser Kestrels breed, along with the use of pesticides in city parks, could seriously affect the breeding population of Jerusalem.

The number of successful nests in Jerusalem has been declining at least since 1999 (Table 3). Until then the number of nests at the beginning of the breeding season (pairs seen courting, mating and laying eggs) was stable at around 80, but in 1999 it was much lower. This was a severe drought year (Fig. 5), and the average productivity for the 35 nests in

![Figure 5. The proportion of successful nests in Jerusalem and the average amount of rain in the years 1997–2001.](image-url)
which young were raised was 1.29 nestlings per nest. This is considerably lower than the average of around two nestlings per nest in the other study years and it does not include another 47 nests that failed totally in that year. Furthermore, productivity in Jerusalem was higher in 1998 (1.91 nestlings) than in 1999 (1.29) ($t_{53} = 3.71, P < 0.001$). The low breeding success in 1999 probably resulted from the low rainfall, which reduced food availability.

The amount of rainfall in winter 1998/99 was much lower than the long-term average, especially in eastern and northern parts of the country (38% and 52% of the average rainfall in Jerusalem and Alona, respectively). The largest difference in rainfall that year between Jerusalem and the Alona area was in December, when the average monthly rainfall was 120–140% in the Alona area, but only 20% in Jerusalem (Meteorology Service in Beit Dagan). This would explain why, in Alona, no significant difference in breeding success was found among years, whereas a large difference was found in Jerusalem.

The number of nests during 2000 and 2001 was probably affected by the failure to raise young in 1999, associated with the severe drought and eventually reducing the breeding population size in the following years. Hence, although the proportion of successful nests in 2000 and 2001 was higher than in 1999, the actual number of successful nests remained significantly lower than in 1997 or 1998. Our conclusion is that the urban breeding population in Jerusalem is highly sensitive and fragile, as one drought-year could have caused a steep decline in the population. Indeed, the Lesser Kestrel breeding population in Jerusalem has declined by 30% in the past 4 years, mainly because of one drought year in 1999.

Stochastic processes such as drought years may cause food stress. Birds in general are very sensitive to food stress, which can affect their physical condition, as has been shown for migrating Steppe Buzzards *Buteo buteo* (Gorney & Yom-Tov 1994). As well as causing this decline in breeding success, stochastic processes can also affect the local population dynamics of food-stressed populations (in this case, urban populations). This might be especially true for Lesser Kestrels if colonies cannot recover through the recruitment of immigrants because of the species’s poor ability to disperse among colonies and patches (Serrano et al. 2001).

This study mainly suggests the reasons for the decline of an urban Lesser Kestrel population. We have too few data on the Lesser Kestrel to explain its population decline in the rural and natural areas or determine the causes for the drastic decline in the past 50 years. Most of the rural Lesser Kestrel populations are located in agricultural areas where pesticides are in use. No research has recently been done on the effect of pesticide residues on the Lesser Kestrel population, but previous research in Israel (Mendelsohn 1972) has shown that pesticides had a very deleterious impact on raptors, especially during the 1950s, and it is reasonable to assume that Lesser Kestrels are sensitive to pesticides whether it is in urban (Gancz et al. 2000) or in rural areas (Mendelsohn 1972). In addition, many of the Lesser Kestrels in the rural areas have started to use nesting boxes that have been erected in the last 5 years, instead of under tiled roofs. It is possible that the massive renovations of roofs and houses in this area have also contributed to the population’s decline and that the new nesting boxes have improved breeding conditions for Lesser Kestrels. There is even less information on the Lesser Kestrel’s situation in the natural areas, but it is known that poaching of Lesser Kestrel eggs and nestlings, especially by the Arab population, exists in these areas. For example, during the 2003 breeding season several nestlings were taken from a Lesser Kestrel colony that breeds on the cliff of the Mar–Saba Monastery. The Judean desert Lesser Kestrel colony in this research also suffered from major human disturbance and, as most of the nests were disturbed, this colony never totally recovered.

This study suggests that a small urban population like that in Jerusalem is not only affected by pesticide use and by the urban development that reduces food availability, but that it also experiences great fluctuations in population size as a result of natural, stochastic events such as lack of rain. If the Jerusalem case is representative of urban populations of Lesser Kestrels in general, then the future of Lesser Kestrels in urban habitats is not promising. Therefore, priority should be afforded to the preservation of rural and natural populations.

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