Impact of Dominant Predators on Territory Occupancy and Reproduction of Subdominant Ones within a Guild of Birds of Prey

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Abstract: The study upon which this article is based examined the interspecific relationships between three different-sized species, both before and during breeding, within a guild of birds of prey in southern Finland between 1997 and 2007. The study sought to examine how the territory occupancy and fledgling production of the smaller (subdominant) species was related to the vicinity of a larger (dominant) species. Inverse relationships were thought to suggest effects of potential intraguild predation. Three key relationships emerged. Firstly, the vicinity of the dominant eagle owl had no significant effect on the occupancy of nesting territories of the subdominant northern goshawk, while the fledgling production of the goshawk increased as the distance from the dominant owl species increased. Secondly, a significant positive relationship was found between the occupancy of the nearest neighbour nesting territories of the eagle owl and the tawny owl. However, the vicinity of the eagle owl had no significant effect on tawny owl reproduction. Thirdly, the occupation of tawny owl territories showed a nearly significant association with the nesting territories of the northern goshawk. However, no significant relationship was found between the vicinity of nearest neighbour nesting territories of the northern goshawk and fledgling production of the tawny owl. The results of this study suggest that depressing reflections of intraguild predation may be expected when the populations of guild members share similar nest sites or if the nest sites of subdominant members of the guild are accessible for dominant members, or in locally unstable populations of less site-tenacious species that show rapid turnover of individuals rather than in strictly site-tenacious long-term territorial species.

Keywords: Diet overlap, interspecific association, intraguild predation, nest site requirements, spacing of territories.

INTRODUCTION

Many predatory species act both as potential competitors and predators for each other or for other species of similar foraging habits [1, 2]. The intraguild predation relationships in vertebrates are usually asymmetrical and size-based, with larger, dominant species preying on smaller ones [3-6]. Based on the available prey lists, intraguild predation is a widespread phenomenon among various birds of prey, particularly among some of the largest ones [3, 7]. However, birds of prey seemed to be occasional and uncommon prey for other birds of prey compared with their principal prey [8-11]. This general scarcity of intraguild predation suggests that the rate at which birds of prey are taken by other birds of prey is roughly proportionate to their availability. However, predation pressure on a prey species may also be intense when the actual mortality by predation is low [12-14]. Mortality may be low because of the effectiveness of predator avoidance, which may limit the habitat available to the prey [4, 6].

Despite potential intraguild predation, the territory occupancy and breeding success of smaller species of the guild in the vicinity of larger species may be similar to that of territories situated further away (cf. [6, 15]). Predation avoidance might be a local form of adaptation that results from the long-term and persistent coexistence of highly site-tenacious and potentially long-lived species, as well as the generally limited availability of suitable nest sites [16] (cf. also [10]). Any impacts that did emerge would be most likely to do so among species of similar activity patterns and most overlapping diets and, hence, potentially overlapping foraging areas [3, 6, 15]. Any effects that dominant predators had on the reproduction of subdominant ones during breeding should be stronger on the species of easily accessible nest sites than on those species whose nests are inaccessible or difficult for predators to access. Because the occurrence and breeding of birds largely depends on the availability of food [17, 18], the impacts of variations in the general food supply probably are also intertwined with the intraguild predation relationships.

In Europe, the eagle owl *Bubo bubo* (Linnaeus 1758), the largest species of owls, preys on various kinds of mammalian and avian prey, while the northern goshawk *Accipiter gentilis* (Linnaeus 1758) is the principal diurnal predator of medium-sized birds; both species are among the most effective predators on other birds of prey [3, 7, 9, 11, 19, 20]. Both of these species have been shown to have depressing effects on populations of some smaller-sized species of birds of prey [5, 6, 10, 21, 22]. The effect of the eagle owl on the medium-sized tawny owl (Linnaeus 1758) has been reported to lead to lower breeding output and spatial gaps in distribution, which indirectly favours other owl species that were potential intraguild prey for tawny owls [6].

In southern Finland, there is a large overlap in the distribution ranges of the eagle owl, the northern goshawk and the tawny owl [23-25]. The occurrence of these species

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is considerably affected by direct or indirect human influence. The eagle owl suffered a previous decline due to heavy persecution [26] but its population later increased thanks to its improved protection status, the super-abundant food supply provided by the rat populations of rubbish dumps, and the increase of open foraging habitats in clear-felled forests, which also provided an increased number of potential nest sites [16, 27].

Earlier findings have suggested that avoidance of the eagle owl might affect the spatial structure of the assemblage of the species studied [16]. The northern goshawk did not display such an effect. Accordingly, four results were expected. Firstly, territory occupancy and reproduction of smaller species in the vicinity of a larger species would not necessarily differ from that of territories situated further away. Secondly, any differences that did emerge would probably exist in occupancy of the two owl species of similar activity patterns. Thirdly, direct effects would be stronger on nestlings in open nests of the northern goshawk than in hole nests of the tawny owl, and, fourthly, would probably occur in poor food conditions influenced by hard winters. In the case of both subdominant species, total losses of clutches or broods could be expected if actual predation was directed to parent birds.

MATERIAL AND METHODS

The Guild of Birds of Prey of the Study Area

The present study area (ca. 800 km^2) is situated in Uusimaa, near the southern coast of Finland (60°N, 25°E). The area consists of rural habitats of mixed fields and forests, as well as Finland's urban capital district. Even in the region's towns, the built-up areas are quite fragmentary and still largely surrounded by relatively rural habitats. Although urban and suburban habitats predominate overall, there are also some relatively large forest tracts, particularly in the eastern half of the study area.

The present study examined interspecific relationships between territorial birds or pairs of the eagle owl, the northern goshawk and the tawny owl, both before and during breeding of the subdominant species within a guild of birds of prey that included six other species with more or less overlapping diets [16]. In addition to the considerable overlap in their diets [28, 29], these three species occupy a wide range of similar habitats, although their preferences differ to some degree. Eagle owls occupy various kinds of semiopen habitats in the study area, while northern goshawks prefer old spruce forests and tawny owls opt for rich deciduous and mixed forests, preferably near eutrophic waters [16]. The birds' preferred territories are obviously their traditional ones, but the preference order of locations is not as obvious. From a single case, therefore, it is not generally possible to find out if the selection of the nesting place is due to pure preference of resources provided or if it is affected by some external force, such as the vicinity of a potential predator. Despite some overlap in habitats between the eagle owl, the northern goshawk and the tawny owl, their nest sites in the study area are totally different. Eagle owls nest on the ground, usually on cliffs or other reasonably elevated places, while goshawks use open twig nests in large trees and tawny owls breed in large hollows in trees (a naturally scarce resource that has nowadays been largely replaced by artificial nest boxes). There is no competition between the species for these nest sites.

The data used here originates from a long-term monitoring programme of birds of prey, the basic work of which was initiated in the 1980s [16], and which covers the period from 1997 to 2007. Nesting territories (*sensu* [7]) and nests of owls were localised, mainly in early spring, by listening for hooting males and later by checking potential nest sites. Similarly, territories and nests of diurnal birds of prey were localised by listening for calling birds throughout the breeding season, checking the known potential nest sites and searching for new ones in suitable habitats [30].

The total number of nesting territories considered in this study was 24 for the eagle owl, 36 for the northern goshawk and 146 for the tawny owl. However, only some of them were occupied each year (Table **1**). Some nesting territories situated near (< 1 km) the boundaries of the searched area were excluded from analysis because of the uncertain locations of their nearest neighbours. During the study period, the number of occupied territories (Table **1**) showed a significant increasing trend in each species ($r_S > 0.840$, $P < 0.001$). This was at least partly explained by the recently increasing tendency of the species to occupy urban nesting habitats [31]. The correlations between the numbers of the species were all positive ($r_S > 0.758$, $P < 0.006$).

Table 1. Number of Nesting Territories Ascertained as Occupied each Year in each Species Studied

Year	*Bubo bubo*	*Accipiter gentilis*	*Strix aluco*
1997	6	8	37
1998	8	10	35
1999	8	10	30
2000	11	11	30
2001	8	11	44
2002	10	10	50
2003	17	15	61
2004	11	13	48
2005	16	18	74
2006	18	19	85
2007	15	28	79

Explaining Interspecific Relationships

The potential effects of the larger predators on the smaller ones were examined based on the annual occupancy of nesting territories, as well as fledgling production of the smaller species in relation to the distance from the nest or other centre of territorial activity of the larger species. The distances between the nest sites of the species, which could also partly reflect the strength of the predator avoidance, were measured from maps to the nearest 100 m. Occupancy of territories was determined by repeated or regular occurrence of single individuals or pairs of birds or by active nests found. Breeding success and fledgling production in

territories of subdominant species was estimated on the basis of nearly fledged young in nests visited for ringing [31, 32].

Food and Weather Variables

The general availability of food for the eagle owl and tawny owl was characterised by indices of vole abundance, which reflects the level of annually fluctuating supply of small voles (here mainly *Microtus agrestis* (Linnaeus 1761) and *Myodes glareolus* (Schreber 1780)), which are of crucial importance for the onset of breeding in Finnish owls (e.g. [33]). The vole abundance indices (individuals/100 trap nights) were based on snap trappings of 384 trap nights each [34]. They were conducted each spring (May) and autumn (October) at 64 standard points of three traps along four catching lines for two nights in Lohja and Kirkkonummi, approximately 30 kilometres west of the present study area. The means of the catches from the preceding autumn and the following spring served as annual indices of vole abundance before the breeding season of owls. In general, the regional vole abundance is clearly reflected in the territory occupancy and breeding of owls of the district [18, 32].

Food availability for the northern goshawk, as well as alternative prey for the owl species, was characterised by the indices of regional late winter abundance of terrestrial birds derived from a national monitoring programme of the Finnish Museum of Natural History (data provided by R. A. Väisänen). The most pronounced fluctuations in the winter bird abundance were due to varying occurrence of the Fieldware *Turdus pilaris* Linnaeus 1758 and the Waxwing *Bombycilla garrulus* (Linnaeus 1758) that followed the pronounced variations in the annual availability of rowan berries (e.g. [18]).

The general features of weather during the preceding winter were characterised by the winter indices of the North Atlantic Oscillation (NAO) [35]. Among other things, the positive values of the winter NAO index (which included December, January, February and March; http://www.cru.uea.ac.uk/cru/data/nao.htm) indicate milder and wetter winter weather in the Nordic countries [36].

Statistical Procedures

Groups were compared by one-way analysis of variance, using the Holm-Sidak test for pairwise multiple comparisons [37]. Linear mixed-effect models were used to analyse the possible effects of the vicinity of dominant predators on the annual occupancy of nesting territories and offspring production of subdominant species [38]. The fixed effects in various analyses included the occupancy and distance of the nearest neighbour territories of dominant predators as well as indices of food availability and weather conditions. The location of territory and the year were random effects. The analyses were conducted using the nlme statistical software package [39, 40].

RESULTS

The mean nearest neighbour distances varied in accordance with size of the species (Table **2**). There were significant differences between intraspecific and interspecific nearest neighbour distances in the eagle owl ($F_{2, 124} = 23.88$, $P < 0.001$) and the northern goshawk ($F_{2, 146} = 36.40$, $P < 0.001$) but not in the tawny owl ($F_{2, 297} = 1.80$, $P = 0.167$).

Table 2. Intra- and Inter-Specific Nearest Neighbour Distances (km) between Simultaneously Occupied Nests or other Activity Centres in Nesting Territories of Three Species of a Guild of Birds of Prey in Southern Finland. Mean (± SD) and Minimum (Min) Values are Given, as well as the Number (N) of Pairs of Locations Considered

Species	Mean ± SD	Min	N
Eagle owl *Bubo bubo*	3.8 ± 2.1	2.6	24
Northern goshawk *Accipiter gentilis*	3.1 ± 1.0	1.7	36
Tawny owl *Strix aluco*	1.8 ± 0.6	0.8	146
Northern goshawk *vs.* eagle owl	4.2 ± 2.8	0.5	31
Tawny owl *vs.* eagle owl	1.9 ± 0.7	0.2	72
Tawny owl *vs.* northern goshawk	1.7 ± 0.7	0.1	82

The vicinity of the dominant eagle owl had no significant effect on the occupancy of nesting territories of the subdominant northern goshawk ($P > 0.05$) (Table **3**), while the fledgling production of the subdominant species increased with the distance from the dominant species ($t_{114} = 2.523$, $P = 0.013$) (Table **4**). Although there was a significant positive relationship between the occupancy of the nearest neighbour nesting territories of the eagle owl and the tawny owl ($t_{390} = 2.839$, $P = 0.005$) (Table **5**), the vicinity of the dominant species had no significant effect on the number of fledged young of the subdominant species ($P > 0.05$) (Table **6**). The occupancy of tawny owl territories showed a nearly significant association with nesting territories of the northern goshawk ($t_{171} = -1.942$, $P = 0.054$) (Table **7**), but there was no significant relationship between the vicinity of nearest neighbour nesting territories of the northern goshawk and the fledgling production of the tawny owl ($P > 0.05$) (Table **8**). The food and weather variables examined showed no sig-

Table 3. Linear Mixed-Effects Model Results on the Effects of Vicinity of the Eagle Owl, as well as Some Annual Food and Weather Factors (Fixed Effects) on the Occupancy of Nesting Territories of the Northern Goshawk in the Present Study Area in Southern Finland, 1997–2007. N = 144 Observations, 11 Groups; the Location of Territory and the Year were Random Effects

	Value	SE	df	*t*	*P*
(Intercept)	0.711	0.171	131	4.154	< 0.001
Eagle owl occupancy	-0.025	0.103	131	-0.245	0.807
Eagle owl distance	0.017	0.014	131	1.222	0.224
Vole abundance	-0.008	0.014	7	-0.541	0.606
Winter bird abundance	-0.000	0.000	7	-0.296	0.776
Winter NAO	0.033	0.059	7	0.552	0.598

nificant relationships with the territory occupancy or fledgling production of the species considered (P > 0.05).

Table 4. Linear Mixed-Effects Model Results on the Effects of Vicinity of the Eagle Owl and Some Annual Food and Weather Factors (Fixed Effects) on the Reproduction of the Northern Goshawk in the Present Study Area in Southern Finland, 1997–2007. N = 127 Observations, 11 Groups; the Location of Territory and the Year were Random Effects

	Value	SE	df	*t*	*P*
(Intercept)	0.818	0.621	114	1.318	0.190
Eagle owl occupancy	0.116	0.343	114	0.337	0.737
Eagle owl distance	0.121	0.048	114	2.523	0.013
Vole abundance	0.006	0.054	7	0.108	0.917
Winter bird abundance	-0.000	0.000	7	-0.849	0.424
Winter NAO	0.053	0.223	7	0.239	0.818

Table 5. Linear Mixed-Effects Model Results on the Effects of Vicinity of the Eagle Owl and Some Annual Food and Weather Factors on the Occupancy of Nesting Territories of the Tawny Owl in the Present Study Area in Southern Finland, 1997–2007. N = 403 Observations, 11 Groups; the Location of Territory and the Year were Random Effects

	Value	SE	df	*t*	*P*
(Intercept)	0.362	0.144	390	2.506	0.013
Eagle owl occupancy	0.179	0.063	390	2.839	0.005
Eagle owl distance	0.008	0.026	390	0.324	0.746
Vole abundance	0.004	0.012	7	0.347	0.739
Winter bird abundance	0.024	0.022	7	1.065	0.322
Winter NAO	-0.008	0.010	7	-0.790	0.456

Table 6. Linear Mixed-Effects Model Results on the Effects of Vicinity of the Eagle Owl and Some Annual Food and Weather Factors on the Reproduction of the Tawny Owl in the Present Study Area in Southern Finland, 1997–2007. N = 238 Observations, 11 Groups; the Location of Territory and the Year were Random Effects

	Value	SE	df	t	P
(Intercept)	0.949	0.526	225	1.805	0.072
Eagle owl occupancy	0.015	0.308	225	0.048	0.962
Eagle owl distance	-0.128	0.150	225	-0.854	0.394
Vole abundance	0.005	0.004	7	1.273	0.244
Winter bird abundance	0.005	0.003	7	1.471	0.185
Winter NAO	-0.001	0.002	7	-0.866	0.415

Table 7. Linear Mixed-Effects Model Results on the Effects of Vicinity of the Eagle Owl and Northern Goshawk Nesting Territories, as well as Some Annual Food and Weather Factors on the Occupancy of Nesting Territories of the Tawny Owl in the Present Study Area in Southern Finland, 1997–2007. N = 185 Observations, 11 Groups; the Location of Territory and the Year were Random Effects

	Value	SE	df	*t*	*P*
(Intercept)	0.874	0.167	171	5.234	0.000
Eagle owl distance	0.003	0.052	171	0.061	0.951
Northern goshawk distance	-0.009	0.004	171	-1.942	0.054
Vole abundance	-0.005	0.012	8	-0.458	0.648
Winter bird abundance	0.001	0.001	8	0.615	0.555
Winter NAO	-0.000	0.000	8	-0.468	0.652

Table 8. Linear Mixed-Effects Model Results on the Effects of Vicinity of the Active Territories of the Northern Goshawk, as well as Some Annual Food and Weather Factors on the Fledgling Production of the Tawny Owl in the Present Study Area in Southern Finland, 1997–2007. N = 270 Observations, 11 Groups; the Location of Territory and the Year were Random Effects

	Value	SE	df	*t*	*P*
(Intercept)	1.034	0.480	257	2.156	0.032
Northern goshawk distance	-0.079	0.130	257	-0.610	0.542
Vole abundance	0.053	0.077	8	0.695	0.507
Winter bird abundance	0.042	0.040	8	1.061	0.320
Winter NAO	-0.102	0.164	8	-0.624	0.533

DISCUSSION

Potential intraguild predation seemed to have no significant effects on the spacing of occupied nesting territories. The impact of intraguild predation on territory occupancy could be due to actual predation on territorial birds or to predator avoidance. The effects on breeding success and fledgling production could be due to predation on nestlings and/or adults. Due to the different kinds of nest sites of the species in the present study area, the potential effect of competition for nest sites could be excluded from the exlanatory factors. Because of some gaps in the annual data, the analyses were based on single interspecific groups of territories. This kind of approach also seems to account for local conditions better than indices that summarise changes in spatial distributions of whole populations.

Indications of Potential Intraguild Predation and Other Associations

The results suggest that predation by the eagle owl may have an effect on the fledgling production of the northern

goshawk. There were no other indications of the potential effects of intraguild predation. This result is in accordance with the expectation that effects on nestlings should be stronger in open nests of the northern goshawk than in hole nests of the tawny owl. The most intense predation pressure on nests of tawny owls, and probably also goshawks, of the study area was derived from the pine marten *Martes martes* (Linnaeus 1758) (T. Solonen, unpublished data). In the highly stationary species of the present guild of avian predators, the direct effects of intraguild predation were expected to occur in poor food conditions after hard winters. However, the indicators of food availability and weather conditions used in the present study did not suggest this.

In general, depressing effects of potential intraguild predation can be expressed especially when the populations of guild members share similar nest sites that are accessible both for dominant and subdominant members of the guild [6, 10, 21, 41]. In the Alps, the eagle owl and tawny owl use similar nest sites that are accessible for both species [6]. Of the nest sites of the minor species in the present Finnish case, however, only those of the goshawk were accessible (but not used for breeding) for the larger species (cf. [21]). Therefore, although the Finnish eagle owls may sometimes catch nestling goshawks, they can have no direct effect on the survival of tawny owl nestlings. However, breeding adults and fledged young of the both subdominant species may be vulnerable (e.g. [11]; T. Solonen, unpublished data). Furthermore, goshawk predation on tawny owl fledglings may be heavy after the owlets have left the safe nesting hole (e.g. [42]; T. Solonen, unpublished data). Actual intraguild predation is probably at its heaviest during the relatively long period between the fledging of young birds and their independence, when they are both inexperienced and loud and then conspicuous and especially vulnerable. In tawny owls, survival during the post-fledging dependency period has been shown to primarily be a function of variation in predation pressures, particularly from raptors [42]. Predation on full-grown birds is probably at its heaviest during winter and before breeding season, when the availability of staple prey is generally at its worst.

Contrary to expectations, there were no indications of predator avoidance or actual intraguild predation in territory occupancy and fledgling production of the tawny owl in the vicinity of the eagle owl. In fact, tawny owls seemed to occupy territories and reproduce successfully near the nesting territories of eagle owls. This was probably due largely to the spatial distribution of resources (local prey supply) that each owl species preferred. The nearly significant association in the occupancy of tawny owl territories with nesting territories of the northern goshawk suggests a preference on similar habitats (fertile mature forests). It is probable that tawny owl occupation, even within the core areas of territories of dominant predators, mainly reflects variations in food supply. In determining the occupation of a territory around a suitable nest site, the availability of food at the right time could be a more important factor than the risk of potential intraguild predation. The role of local circumstances, such as the availability and quality of alternative nest sites, still seemed to be of crucial importance.

For various reasons, even territories in the most preferred habitats were left unoccupied in some places. However, the roles of interspecific relationships and other possible factors could not be either verified or ruled out. Based on circumstantial observations, annual shifts of nest site of the eagle owl within a territory were sometimes followed by respective shifts in the location of a nest site in a nearby territory of the northern goshawk, so that a minimum distance of approximately one kilometre between the nests of species was maintained. Goshawks can breed successfully, even at that distance from the eagle owl nest. Tawny owls, on the other hand, seemed to avoid shifts of nesting locations of the eagle owl, but not by far. The reaction of tawny owls to the northern goshawk appeared somewhat different. Both goshawks and tawny owls preferred mature forests. This sometimes seemed to lead to nearby nestings of the species because preferred fertile mature forests were considerably rare and a continuously decreasing resource in the study area. In some extreme cases, successful nestings of tawny owls were recorded only a few dozen metres from an active nest of the northern goshawk. In addition to similar habitat preference, an explanation of nearby nestings might be some kind of benefit gained. Various species of birds seemed to benefit from the vicinity of other species that may alert an area of potential hazards or defence against predators [43-48]. Similar relationships may occur also within guilds of predators that, in some other situations, could harm each other [49].

The effects of intraguild predation depend both on the character of the predator and the behaviour of the prey. In the case of a generalist predator, the effect of predation on a prey population should be relatively weak if various other kinds of prey are available and predation is not selective (e.g. [11, 50]). This kind of intraguild predation should not have a pronounced effect on the diversity within the guild (cf. [6]). In contrast, the effect of a selective or specialist predator might be considerable. This could also be the case when predation pressure is high due to the relative scarcity of other kinds of prey and when the subdominant species have minimal opportunities to find suitable refugia to avoid predation [5, 11] (cf. also [6, 10]). Between the most used core areas of a predator's home range, there are often parts of less intense occupation and predation that might provide such refugia [6]. However, in addition to territorial birds, there are also less visible and less audible subpopulations of non-breeding floaters (e.g. [22, 51]) that probably largely use those parts of terrain that are less used by territorial birds. Thus, the predation pressure by a predator population may be spatially much more evenly distributed than expected on the basis of territorial birds only.

CONCLUSIONS

When a dominant species within a guild of birds of prey occupies a territory that overlaps the territory of a subdominant species, the latter may either stay or leave. A subdominant species that is establishing a new territory may avoid the vicinity of a dominant species. Alternatively, it may occupy a territory independently of the dominant species or it may actively seek out the territory of another species in order to achieve some advantage. Thus, the order of establishing overlapping territories affects the initial interspecific response of the subdominant species. The effects of possible intraguild predation on the territory occupancy of subdo-

minant species can vary depending on the pair of species considered, and can also vary locally. This variation may be due partly to variations in resource supply and the way in which the species share common resources. Spatially uneven distribution of essential resources may also lead to quasi-significant associations between dominant and subdominant members of the guild. High frequency of occupation of long-term nesting territories in the vicinity of dominant predators suggests that those territories are traditional, especially tempting and of high quality, and/or that their occupants are well-adapted to living in such conditions despite the proximity of predators that are capable of killing them.

Depressing effects of intraguild predation may be expected when the populations of guild members share similar nest sites that are accessible for dominant and subdominant members of the guild, or in locally unstable populations of less site-tenacious species that show rapid turnover of individuals rather than in strictly site-tenacious long-term territorial species. A seemingly minor effect of intraguild predation on the territory occupancy of subdominant species may be due to abundant floaters that readily fill the gaps caused by predation. This can only be studied by monitoring individually recognisable populations. The survival of fledged young can be monitored by intensive auditory observations or by telemetry. The mortality of fully-grown birds due to intraguild predation could be studied in large-scale (for example, nation-wide) ringing programmes by analysing the survival data of ringed birds originating from different distances from nests of dominant predators.

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