A top predator provokes similar defense behavior as a mesopredator in an intraguild prey

Kai-Philipp Gladow[1], Marla Jablonski[1], Nayden Chakarov[1,2], Oliver Krüger[1,2]

[1] Department of Animal Behaviour, Bielefeld University, Bielefeld, Germany

[2] Joint Institute for Individualisation in a Changing Environment (JICE), University of Münster and Bielefeld University, Bielefeld, Germany

Corresponding Author: Kai-Philipp Gladow, ORCID: 0000-0003-0142-7383

E-mail: kai-philipp.gladow@uni-bielefeld.de

Acknowledgements: We thank Georgios Drosopoulos for his help during data collection in the field and Tim Maximilian Rapp, Hugo Perreira, Meinolf Ottensmann and Tony Rinaud for helping to sample nest locations. We further thank Ingo Höpfner from the Naturkunde-Museum (namu), Bielefeld, and Till Töpfer from the Zoological Research Museum Alexander Koenig (ZFMK), Bonn, for providing the taxidermic models of goshawks, Marléne Baumeister for statistical recommendations and Barbara A. Caspers for her helpful advice during the writing process.

Conflict of interest statement: The authors have no competing interests to declare that are relevant to the content of this article.

Data Availability: The raw data associated with this article have been uploaded to the sciebo data server and are available via this link: https://gitlab.com/KPG13/public

Funding statement: This work was supported by the Friedrich-Ebert-Stiftung (FES) to KPG and the German Research Foundation (DFG; project number 398434413), as part of the SFB TRR 212 (NC^3; project numbers 316099922 and 396780709) to OK and NC.

Ethics approval statement:All observations and experiments were conducted without touching or capturing any of the participating birds and during their regular breeding events. Thus, we did not need a specific ethics permission according to national guidelines.

Author contributions: **Kai-Philipp Gladow** (Conceptualization [Lead], Data Curation [Lead], Formal Analysis [Lead], Funding Acquisition [Equal], Investigation [Equal], Methodology [Lead], Project Administration [Lead], Resources [Supporting], Software [Lead], Supervision [Equal], Visualization [Lead], Writing - original draft [Lead], Writing - review & editing [Equal]); **Marla Jablonski** (Conceptualization [Supporting], Data Curation [Supporting], Investigation [Equal], Methodology [Supporting], Writing - review & editing [Equal]; **Nayden Chakarov** (Data Curation [Supporting], Funding Acquisition [Equal], Investigation [Supporting], Project Administration [Supporting], Resources [Lead], Supervision [Equal], Writing - review & editing [equal]); **Oliver Krüger** (Conceptualization [Supporting], Funding Acquisition [Equal], Methodology [Supporting], Resources [Supporting], Supervision [Equal], Writing - review & editing [Equal])

Abstract

The loss of top predators has been shown to lead to drastic changes in community structure. An important part of this is the shift in behavior of other species. The understanding of such changes is scarce because recordings of behavioral reactions towards lost species are rarely done. This is important for predators experiencing predation pressure themselves, known as intraguild predation. Re-colonizations offer the unique possibility to fill this knowledge gap. However, only a few studies tested experimentally how subordinate predators change their behavior towards top predators in comparison to other members of their guild. Birds adjust the level of nest defense in response to perceived threats. Therefore, we expected birds of prey in intraguild predation systems to show an appropriate level of nest defense against the predator they are faced with, with the highest level shown against the top predator. We tested this by placing models of eagle owls (*Bubo bubo*) and goshawks (*Accipiter gentilis*) close to nests of common buzzards (*Buteo buteo*) and measured the reaction. Additionally, we compared the development of the three populations and tested for other influences on the defense behavior. We did not find significant differences in aggression by common buzzards toward eagle owl and goshawk and therefore conclude that the top predator provokes a similarly high nest defense as another (meso-)predator. This shows that in ecological communities the top predators and mesopredators may not have separated levels from the viewpoint of intraguild prey. Top predators and mesopredators might be perceived as comparable threats.

Significance Statement

When predators re-colonize an area, they affect how their competitors and potential prey behave. We studied how smaller raptors, like common buzzards, react to bigger predatory birds. We expected buzzards to defend nests more aggressively against the biggest predator. Our tests did not fully confirm this expectation. Different predators appear to influence the behavior of subdominant competitors similarly. This challenges our current understanding of interactions within food webs.

Keywords: Intraguild predation, birds of prey, top predator, defense behavior, eagle owl

Introduction

A central task of community ecology is to identify the species, traits and behaviors which shape the composition of an ecological community (McPeek 2017; Mittelbach and McGill 2019). Top predators, i.e. carnivorous species that do not have any natural predators themselves, are often considered to have a major influence on ecological communities (Mueller et al. 2016; Terraube and Bretagnolle 2018). Presence or absence, (re-)introduction or loss of top predators lead to substantial differences and changes in species composition and habitat use of animals in communities (Chakarov and Krüger 2010; Ripple et al. 2014). This holds especially true in the context of intraguild predation (IGP), where top predators not only kill and eat mesopredators, but also compete with them for the same resource, such as food (Polis et al. 1989). Theoretical models as well as empirical studies have shown that interactions within an IGP system have the potential to significantly influence ecological communities (Polis et al. 1989;

Holt and Polis 1997; Ripple et al. 2014; Lourenço et al. 2018). However, research on the effects of re-colonization by avian top predators on mesopredators in an IGP setting is still rare (Terraube and Bretagnolle 2018) and has seldom focused on behavior. This is unfortunate as the behavioral reaction of a mesopredator to a top predator is the first and direct response, before effects on reproduction and/or survival become obvious. In addition, previous studies on IGP often only featured two species, the intraguild predator and one intraguild prey (Sergio and Hiraldo 2008; but see Mueller et al. 2016). This may be insufficient to detect important interactions between different mesopredators in the presence of multiple predators which are also competitors.

Different behaviors like defense strategies, activity levels or search for hiding locations play important roles in predator-prey interactions and constitute always the first line of defense against a predator (Kikuchi et al. 2023; Salazar et al. 2023). Because of their short-lived nature and immediacy, the study of these behavior is often much more difficult than documenting effects further down the line such as reproduction, survival or growth. Nonetheless, behavior clearly influences these traits as a part of individual life-history strategies (Boerner and Krüger 2009; Brust et al. 2013; Schwarz et al. 2022). Several bird species have been shown to adjust their level of aggressiveness against potential predators of their young to the level of the actual threat (Martin et al. 2000; Ibáñez-Álamo et al. 2015). Thus in a complex and asymmetrical IGP system, a mesopredator can be expected to adjust its level of aggression accordingly depending on whether it confronts a top predator or another mesopredator. We tested this key prediction of prey defense theory applied in IGP context, using the common buzzard

(*Buteo buteo*) as model species. Common buzzards and their interactions with other raptorial birds have been investigated in an area in western Germany for over three decades, especially after the Eurasian eagle owl (*Bubo bubo*) re-colonized the area after over 50 years of absence due to human persecution (Boerner and Krüger 2009; Chakarov and Krüger 2010; Krüger 2002a; Krüger 2002b; Mueller et al. 2016). The return of this top predator led to changes in the proportion of failed reproductive attempts, density, territory dynamics and habitat choice of common buzzards and northern goshawks (*Accipiter gentilis*) (Chakarov and Krüger 2010; Mueller et al. 2016). Previous studies have measured the aggressive response of common buzzards towards top predators like eagle owls (Boerner and Krüger 2009; Lourenço et al. 2011; Mueller et al. 2016) and towards other intraguild predators (e.g. northern goshawks, Krüger 2002b). However, this has never been performed simultaneously. To assess the impact of top predators on the behavioral response of a mesopredator, we carried out a direct comparison with the dominant mesopredator. Therefore, we tested the nest defense behavior of common buzzards against eagle owls as top predators in comparison to northern goshawks, the dominant mesopredator, which is still capable of killing young and adult buzzards (Mebs and Schmidt 2014, Björklund et al. 2016). The goshawk was the former avian top predator in the study area for over 50 years before eagle owls re-colonized the area (Krüger 2002b; Chakarov and Krüger 2010; Mueller et al. 2016). Based on the attributed and observed impact of top predators on ecosystem composition and community structure, and the ability of many bird species to adjust their level of aggressiveness towards the perceived threat, we predict that buzzards should show a higher level of aggression when defending their nest against eagle owls in comparison to goshawks.

Methods

Study area

The study area is located west of the city of Bielefeld in North Rhine-Westphalia and Lower Saxony, Germany (52.06 N and 8.30 E). It measures 300 km² in size and includes three different natural regions: the largest part in the north consists of a hilly terrain with mostly rural landscape and small to medium sized deciduous forests (mainly European beech *Fagus sylvatica*); the Teutoburg Forest in the center is a low mountain range with larger forested areas containing predominantly beech as well as European spruce (*Picea abies*); the south is similar to the north, although its dominating tree species is Scots pine (*Pinus sylvestris*) growing on sandy soils. Research on raptors has been done in this study area since 1975, with the main focus on common buzzards since 1989 (Krüger and Lindström 2001). Additionally, northern goshawks, red kites (*Milvus milvus*) and Eurasian eagle owls as well as their interactions have been studied there (e.g. Krüger 2002a; Mueller et al. 2016).

Study species

Common buzzards are the most abundant birds of prey in the western Palearctic (Walls and Kenward 2020). They are medium-sized diurnal raptors with a great variation in plumage coloration ranging from very dark brown individuals to almost white ones and weigh around 800 to 1,000 g with a wingspan of up to 130 cm (Mebs and Schmidt

2014). Common buzzards feed on a variety of different prey items, ranging from small mammals and birds to invertebrates (Walls and Kenward 2020). However, if field voles (*Microtus arvalis*) are abundant, buzzards preferentially hunt them (Mebs and Schmidt 2014). They build their nests in trees often close to the edge of forests with easy access from open areas (Krüger 2002a; Chakarov and Krüger 2010).

In contrast, **northern goshawks** usually breed deeper in the forest and keep a higher distance to forest edges as well as human structures like settlements or roads (Krüger 2002a; Chakarov and Krüger 2010). This and their inconspicuous behavior led to the nickname “phantom of the forest”, but recently, some goshawks have successfully colonized cities like Cologne and Berlin (Merling de Chapa et al. 2020). Goshawks mainly hunt by ambush in dense vegetation, their main prey items consisting of small to medium-sized birds like pigeons (Mebs and Schmidt 2014). They are capable of killing buzzards and hence act as intraguild predators of buzzards, although they kill nestlings far more often than adults (Krüger 2002b; Björklund et al. 2016, Mueller et al. 2016; Walls and Kenward 2020). This dominance is possible because of stronger legs and talons as well as a more compact and massive body, as goshawks have shorter wings (up to 120 cm) and a higher body weight (females up to 2,000 g; Mebs and Schmidt 2014; Sergio and Hiraldo 2008). Males, however, are smaller and lighter and thus may pose as a lesser threat to adult buzzards compared with female goshawks (Mebs and Schmidt 2014). Northern goshawks are distributed in large parts of the Holarctic, thus completely overlapping with the distribution of common buzzards, but not vice versa (Mebs and Schmidt 2014).

Eurasian eagle owls are distributed in Europe and Asia, ranging from boreal forests in the north to the subtropics in the south, excluding the Indian subcontinent and south-east Asia (Scherzinger and Mebs 2020; IUCN 2023). They are the biggest owls in the world with a wingspan of 170 cm and a body weight of around 3,000 g (Scherzinger and Mebs 2020). This is also reflected in their prey spectrum. During their night-time hunts, they feed on diverse prey, from field voles and small birds up to foxes and also predate on birds of prey (Sergio et al. 2003; Scherzinger and Mebs 2020). Thus, in many ecosystems, they serve as top predators at the top of the food network, especially where wolves, bears and eagles are not common (Lourenço and Rabaça 2006). Eagle owls often breed in quarries or old nests of birds of prey, but they can also breed just on the ground next to a tree (Scherzinger and Mebs 2020).

Breeding density and population dynamics of the three species in the study area

Since 1989, all breeding attempts of birds of prey, including common buzzards and northern goshawks, are being mapped for the whole study area (see Krüger and Lindström (2001). Since 1996, eagle owl breeding attempts have been mapped as well. There is no knowledge of eagle owls breeding in this area in the preceding years, so recolonization likely started in that year. Breeding pair density of the species investigated were compiled to compare their population trends and densities.

The common buzzard population has increased more than eightfold between 1989 and 2023 (Fig. 1A) from around 12 breeding pairs per 100 km^2 to over 100 breeding pairs per 100 km^2. Equally impressive has been the re-colonization of the study area by eagle owls, from 1 breeding pair per 100 km^2 to a maximum of over 9 breeding pairs per 100 km^2 (Fig. 1B). In slight contrast, the population dynamics of the goshawk show a stable population size with between 5 and 7 breeding pairs per 100 km^2 (Fig. 1B). The densities of the three species are among the highest ever reported (common buzzard, eagle owl) or above average for central Europe (goshawk), making frequent behavioral interactions exceedingly likely.

Aggression experiments - general aspects

Nest mapping started in March 2022. Every forest patch in the study area was checked for active nests and coordinates were recorded. We visited possible active nests several times until we found droppings of hatched chicks.

We carried out experiments during the late breeding season of common buzzards in 2022, i.e. when the chicks had hatched and were fed by both parents in the nest. We used the information gathered during ringing of the chicks about the number and age of nestlings in corresponding broods. Ringing and experiments were done by different team members to record data blind and avoid sampling biases.

Out of all active nests, we selected all which fulfilled the following criteria: easy access with a car, breeding close to the forest edge and having chicks of at least seven days of age. The first two criteria were met by almost all breeding attempts in our area, therefore our sample was representative of the study population (see Methods/Study Area). With the time limit of all chicks having fledged mid of July, we approached 125 nests (80 with eagle owl dummies, 45 with goshawk dummies), more than half of our breeding population in 2022 (see Fig. 1).

Materials

We used four different models (dummies) for our experiments: two were eagle owl dummies (one taxidermic model and one made of plastic) and two were goshawk dummies (one adult female and one sub-adult female goshawk, both taxidermic models). The plastic eagle owl was painted and equipped with feathers to resemble a real eagle owl as closely as possible. We did not find a statistical difference in aggression towards dummies of the same species, so for further analysis, we treated the two eagle owl and the two goshawk dummies as equal within species. No playbacks of eagle owls, goshawks nor buzzards were used additionally to attract focal common buzzards. The experiment did not represent any risk to the buzzard individuals involved in.

Experimental procedure

At each nesting site, only one trial was conducted, either with one of the eagle owl dummies or with one of the goshawk dummies. Thus, we did not perform repeated trials per brood.

Experiments were carried out between 4th of June until 8th of July 2022. After arrival at a nesting site, we placed one of the dummies on a tripod close to the forest edge in 50-80 m distance to the buzzard nest. We returned to the car and waited for 30 minutes if at least one of the adult buzzards would appear in sight, otherwise we moved to the next territory. When a buzzard appeared and had a clear view of the dummy, we started the behavioral observation which lasted for 30 minutes as well. The buzzard’s reaction to the dummy was measured by recording the following behaviors: general aggression (scored from 0 to 3), direct attacks (with physical contact between the buzzard and the dummy), latency of directly attacking and number of mock attacks ("mock charges", without physical contact between buzzard and dummies; see table 1 for detailed description of categories). We also recorded the date, time, trial number, territory name, individual nest number, and dummy used (ID and species).

Trials were stopped before reaching the 30 minutes limit in case buzzards started to attack the dummy physically (score = 3 (maximum), direct attack = yes) to prevent especially the taxidermic models from damage, which would have made them unusable for further trials. Hence, when we compared mock charges between trials in our analysis, we corrected for trial length because some trials with mock charges also included direct attacks and thus were shorter than 30 min.

To control for other possible influences on the aggression level, we measured the distance to the closest breeding eagle owl or goshawk pair respectively, as well as the number of offspring, the intensity of parental response while climbing the nest to ring the nestlings, and the wing length of the oldest hatchling as a proxy for age. Nestling wing length correlates strongly with age and thus serves as a good proxy measurement for hatching date (Bijlsma 1999). The parental response during ringing of the chicks was scored with five different levels (no reaction - fleeing - circling and calling - coming closer than 20 m - attempting a charge on the climber). Number of offspring varied between 1 and 3 hatchlings per nest. Distance to the next breeding eagle owl pair varied between 0.58 km and 4.61 km, to the next breeding goshawk pair varied between

0.11 km and 5.57 km. Each included buzzard pair was tested with one dummy species only (eagle owl or goshawk, not both).

Statistical analysis

For the statistical analysis, we used the open-source software R (R Core Team 2021) with the additional packages *MASS, rankFD, ordinal*, *AICcmodavg*, *effsize, rcompanion*, *readODS* and *ggplot2* (Venables and Ripley 2002; Wickham 2016; Torchiano 2020; Christensen 2022; Konietschke et al. 2022; Mazerolle 2023; Schutten et al. 2023; Mangiafico 2024). We performed Brunner-Munzel tests for a rank-based comparison of two independent samples for our main hypothesis (reaction to eagle owl dummies versus reaction to goshawk dummies) and generalized linear models (GLMs) as well as cumulative link models (CLMs) for further analysis of potential effects on the behavior. For model selection, we compared the parsimony of models containing different variables using their AICc.

The Brunner-Munzel test is a non-parametric test which is very robust against great differences in data structure of the two compared samples, like sample size or distribution equality, and also very useful if the data has many outliers, as is often the case in ecological or behavioral data (Konietschke et al. 2022). For the calculation of effect sizes, we used Cliff's Delta for the aggression score, Cohen's h for the proportion of direct attacks and Cohen's d for the attack latency as well as for the number of mock charges, the two latter after logarithmic transformation (Torchiano 2020; Mangiafico 2024).

Results

Descriptive analysis of the behavioral experiments

Out of the 125 territories that we approached for experiments (80 with eagle owl dummies and 45 with goshawk dummies), focal buzzards appeared after presentation of the stimulus in 58 territories (84 individuals reacting), 34 with eagle owl dummies (50 individuals reacting), 24 with goshawk dummies (34 individuals reacting). In 30 trials (51.7% of all territories with reaction), buzzards reacted with a direct attack on the dummy. In seven trials, only mock charges were observed (12.1%), but including trials with subsequent direct attacks, mock charges happened in 27 trials overall (46.6%). In 13 trials, only calling and circling reactions occurred over the dummy (22.4%). In eight trials, no reaction of the focal buzzards was detected although they were flying over or close to the dummy (13.8%).

Considering the different treatment types, we got the following distributions of reactions: using the eagle owl dummies (n = 34), buzzards attacked directly in 20 cases (58.8%), 15 of these 20 also included mock attacks. In four trials (11.8%), buzzards showed only mock attacks without direct attacks. Circling and calling without other reactions was recorded in six trials (17.7%), and in four trials no reaction was detected (16.7%).

For goshawk dummies (n = 24), we observed direct attacks in ten trials (41.7%), five of these ten also included mock attacks. Only mock charges without direct attacks were performed by buzzards in three trials (12.5%). In seven cases, only circling and calling was observed (29.2%). No reaction was recorded in four trials (16.7%).

Defense behavior against top predator vs. mesopredator

Overall, we did not find a significant difference between the buzzard reactions towards the top predator (eagle owl) and the mesopredator (goshawk). A summary of all test results is listed in Table 2.

Although the difference between goshawk and eagle owl trials was rather large with regard to the proportions of direct attacks and "circling and calling" responses respectively, our statistical analysis did not show a significant difference, neither for the aggression score overall, nor for the amount of direct attacks alone (see Fig. 2 and Table 2).

Among trials with direct attacks (score = 3), the median attack latency was 2.5 min (IQR 7.5 min). Eagle owl dummies seemed to be attacked faster (2.0 min, IQR 5.25 min) than goshawk dummies (6.0 min, IQR 9.25 min), but there was no significant difference between the groups (T = -0.875, p = 0.394, Fig. 2).

The median number of mock charges per 10 minutes with eagle owls was 10 (IQR 12.67), with goshawks 5.83 (IQR 8.67). Similar to the other variables, we did not find a significant difference between the treatments (T = 1.541, p = 0.139, Fig. 2). Interestingly, buzzards exerted mock charges in a greater proportion of trials including eagle owl dummies than goshawk dummies (55.9 % vs. 33.3 %).

Despite our large sampling effort, a power analysis revealed that our sample sizes were too small to reach an appropriate level of statistical power of 0.7 or 0.8 (our power level was 0.2). That meant that the risk of keeping the null hypothesis even when it should be rejected was at 80 %. Because of this, we also looked at the effect sizes of our samples. For all four defense behaviors, we only found a *small effect* for higher aggression towards eagle owl dummies. Cliff's Delta for the comparison of the aggression score (centered around 0) was 0.184 (lower CI: -0.105, upper CI: 0.444). Cohen's h for the proportion of direct attacks was 0.345 (-0.179, 0.866). Cohen's d for the attack latency was -0.359 (-1.158, 0.440) and Cohen's d for the number of mock charges was 0.472 (-0.406, 1.350).

Other factors influencing buzzard nest defense

In most of our linear models, other possible effects had only a minor explanatory power for the defense behavior. Age (measured by wing length) and number of offspring were often included in the best models, but even these models only explained a small part of the variation and were not sufficiently better than the null model (see Tables 3, 4 and 6). The only exception were effects on the attack latency where the best model included both age and number of offspring and had an ΔAIC bigger than 2 compared to the null model (Table 5). Buzzards with more and younger hatchlings attacked the dummies faster (see Fig. 3).

Discussion

We found that in an intraguild predation context a subordinate mesopredator did exhibit similar defense behavior against the top predator compared with another mesopredator. This differs from our expectations based on literature and theory dealing with (1) top predator impact on communities, (2) prey behavior, and (3) previous experiments with raptors (Polis et al. 1989; Holt and Polis 1997; Krüger 2002b; Lourenço et al. 2011; Mueller et al. 2016; Salazar et al. 2023). This leads to several implications which we discuss here.

We found no significant difference between the intensity of nest defense behavior of common buzzards against two intraguild predators, Eurasian eagle owls and northern goshawks. In general, the aggression level was high, with more than 50 % of buzzards showing either mock and/or physical attacks for both presented species. This is mostly consistent with similar studies analyzing aggression levels of common buzzards, especially when confronted with eagle owls (Boerner and Krüger 2009; Lourenço et al. 2011; Mueller et al. 2016), but a surprising difference to Krüger (2002). There, buzzards showed only very little aggression against goshawk dummies (only 1 out of 14 pairs performed a physical attack; possible reasons are considered further below).

The population densities observed in our study area - up to 9 pairs per 100 km^2 for eagle owls, over 100 pairs per 100 km^2 for common buzzards and 5-7 pairs per 100 km^2 for goshawks - are among the highest densities ever reported for these species (Mebs and Schmidt 2014, Scherzinger and Mebs 2020, Walls and Kenward 2020). They make behavioral interactions of common buzzards with both eagle owls and goshawks within our study area extremely likely.

Our results question some predictions made by theoretical concepts about intraguild predation and the importance of one single top predator species in these models (Polis et al. 1989; Holt and Polis 1997). In general, predation is often considered as the factor with the biggest influence on community structure, hence the importance of top predators for food webs (Lourenço et al. 2018; Mittelbach and McGill 2019). The role of a top predator in a given community is usually reserved for the biggest species alone, which has no natural enemies and exerts predation pressure without being exposed to it itself (Lourenço et al. 2018; Terraube and Bretagnolle 2018). To our knowledge, this is the first study directly comparing the effect of an top predator on defense behavior with the effect of the second-ranked, or dominant mesopredator in an IGP setting. In other such experiments, either no control was used or the comparison was an IG prey (Lourenço et al., 2011; Mueller et al., 2016). Our results suggest that - even if a species like the goshawk itself can be preyed upon by eagle owls - high-ranked mesopredators may have an impact similar to top predators on subordinate mesopredators. This fits to other results of studies finding a high overlap in breeding habitat characteristics in goshawks and eagle owls, the latter driving out the former after recolonization (Chakarov and Krüger 2010; Mueller et al. 2016), showing the high ecological similarity. The mechanisms of this displacement are still not well understood.

Most IGP models and empirical studies analyze interactions of only two species, a dominant and a subdominant predator or two predators equal in rank (Holt and Polis 1997; Sergio and Hiraldo 2008). This has been helpful to understand the basics of IGP interactions, but since a guild commonly consists of more than just two species, theory and empirical research should strive for a more complete understanding of IGP systems in their complexity (Terraube and Bretagnolle 2018). Our study shows that interactions become more complicated and less coherent with simple predictions when multiple intraguild predators are involved, as is the case in our high-density populations.

Future models of IGP should test how these interactions change if the functional role of top predators is filled by several species. Many theoretical and empirical examples show continuous coexistence of competing species, maintained by seemingly minor differences (Mittelbach and McGill 2019). Such coexistence can be further supported by high within-population variation, co-adaptation (Li et al. 2023), or a patchy environment with intermediate-level disturbances (Sousa 1979; Chesson and Huntly 1997; Chesson 2000). Studying these effects on behavioral traits in IGP contexts would be highly desirable for the future, particularly given the usual rarity of top IGP species and the corresponding difficulties of studying them.

Potential prey species (and individuals) are known to adjust their behavioral defense level according to the predatory threat (Caro 2005, Salazar et al. 2023). It has been shown repeatedly that birds are able to distinguish different predator species by visual cues, including between owls and birds of prey, and their aggression level changes accordingly (see Fuchs et al. 2019 for a review). Without significant differences in the behaviors against the two predator species, it appears that common buzzards do only perceive eagle owls to be scantily more dangerous than goshawks. This might be due to several reasons. We tested buzzards during their chick-rearing period. For buzzard chicks, eagle owls and goshawks both serve as effective predators, so even if there was a difference in danger for adult birds, the high danger for the chicks could lead to a similar nest defense behavior of their parents. In contrast to adults, nestlings cannot leave the area to avoid predation. Thus, defensive behavior of parents might not be regulated by risk for their own survival but rather by the risk for their offspring which is similar between both potential predators (Caro 2005, Ibáñez-Álamo et al. 2015). Another explanation could arise from the different activity times of eagle owls and goshawks. Whereas goshawks are diurnal raptors, eagle owls mainly hunt during twilight and night and hence have adapted to their respective environment (Mebs and Schmidt 2014; Scherzinger and Mebs 2020). Since we conducted our experiments during daytime (when buzzards are active), we cannot completely rule out that a presented eagle owl dummy during daytime is not perceived as a bigger threat than goshawks because 1) it is not the time when eagle owls usually hunt and 2) their sensory system is less adapted to daytime, giving the buzzards an additional advantage (Walls and Kenward 2020). There is some evidence that owls cannot see as well as diurnal birds of prey during daylight, so buzzards might perceive eagle owls as less threatening at daytime (Martin 1986; Potier et al. 2020). This could have reduced the level of aggression towards eagle owls in comparison to diurnally active goshawks. Ironically, the higher share of trials with mock attacks against eagle owls could be attributed to this pattern: Buzzards may dare to swoop closely to the eagle owls more often, possibly because the perceived risk of injury is smaller in comparison to goshawks.

Kikuchi et al. (2023) point out that antipredator defenses can consist of multiple mechanisms when encountering a predator. We only studied one kind of defense mechanism, the direct behavioral reaction towards intraguild predators. We are aware that there can be other adaptations to the respective predators. Individuals often have different defenses because they encounter different predator types. Hence there might be a difference between the two treatments, be it physiological or behavioral (Kikuchi et al. 2023), which we cannot control for, like reduced feeding rates. However, eagle owls and goshawks are both predatory birds with similar feeding ecologies (except goshawks being diurnal and eagle owls being nocturnal) and habitats (Chakarov and Krüger 2010; Mueller et al. 2016). Nest defense is one of the best-studied defense traits in birds and known to vary according to the predatory threat (Caro 2005, Fuchs et al. 2019; Salazar et al. 2023), but did not differ significantly for the two presented threats in our study. Therefore it seems rather unlikely that buzzards differ in other, potentially more subtle and less influential antipredator defenses when confronted with eagle owls or goshawks.

Based on earlier aggression experiments with common buzzards, a bigger difference in nest defense was expected. Although there has been only one empirical study analyzing direct reactions of common buzzard to northern goshawks (Krüger 2002b), the observed aggression was very low, leading to a great contrast to the comparatively high amount of direct and fake attacks in our study. One possible explanation could root in the different methodology: in Krüger's study (2002b), goshawk dummies were placed directly in front of the buzzard's nesting trees inside the forest. Furthermore, playback calls of goshawks were played in addition to the visual presence of the dummy. This was done because Krüger (2002b) was more interested in the general breeding behavior and reproductive success than the actual aggression against predators. Thus, the buzzards had the chance to be aware of a goshawk's presence even before they saw the dummy, potentially leading to a more inconspicuous behavior to avoid being perceived by the predator. This is a common reaction of prey species - if you know where your predator (or the predator of your offspring) is but not vice versa, better stay hidden (Montgomerie and Weatherhead 1988; Lima 1998; Caro 2005). In our study, we deliberately did not use playback calls because of the potential to scare away or warn buzzards of an enemy's presence. Thus, dummies were placed in the open field to be obvious for approaching buzzards. This, however, could have led as well to the relatively rare response with only 58 trials with focal birds appearing out of 125 approaches to nesting sites. We cannot exclude the possibility that a dummy's presence might not have been recognized by all buzzards, whereas playbacks may have improved also the perception of the visual stimulus. Corresponding tests with this study design modification remain to be done and compared.

In general, the other possible influences on the defense behavior that we could control for in the linear models only had a minor influence. Offspring age and number of offspring were included in the best models but even these models only explained a small part of the variation and were not substantially better than the null model. The only exception was the model for attack latency, where younger offspring and higher offspring number both led to faster attacks on the dummies. A higher investment in nest defense with more offspring is congruent with theory (Curio 1987; Caro 2005, Svagelj et al. 2012). With regard to offspring age however, a higher nest defense for older chicks and not the other way around would be expected based on literature; as Caro (2005) points out, a higher aggression level with older offspring is very widespread, even though the underlying mechanisms are not fully understood. However, studies dealing with these questions rarely investigated latency of approach or attack. More research on this to examine differences and similarities with other behavioral reactions, including repeated and longitudinal trials would be highly desirable.

Regarding common buzzard aggression in general, we did not find a consistent dependence of reaction intensity on the age of their offspring and the already allocated investment. In Krüger's study (2002b), the tested individuals were more aggressive against dummies of conspecifics and against goshawks with increasing offspring age, but higher defense for more offspring was only shown when dealing with conspecifics. When similar experiments were performed with dummies of conspecifics and eagle owls a few years later, neither the number nor age of offspring explained aggression levels (Boerner and Krüger 2009). Since all of these studies aimed to answer different questions, an experimental set-up to resolve these contradicting patterns would be worthwhile in the future.

Conclusion

To examine the influence of top predators on ecological communities, it is important to investigate the differences of their impact on potential prey and their behavior in comparison to other predators. In this study, we showed that a subordinate mesopredator did not show strong differences in its nest defense behavior toward the top predator and another dominant mesopredator in the community. This suggests that the danger emanated by top predators may be perceived similarly to the one of other intraguild predators by their intraguild prey. As behavior is one of the first and most direct reactions of animals to environmental change, behavioral reactions should be considered more when estimating the impact of certain species on ecological communities. Especially intraguild predation models and investigations in the wild should incorporate the possibility for dominant mesopredators influencing their intraguild prey in a similar way as the top predators does.

Figures

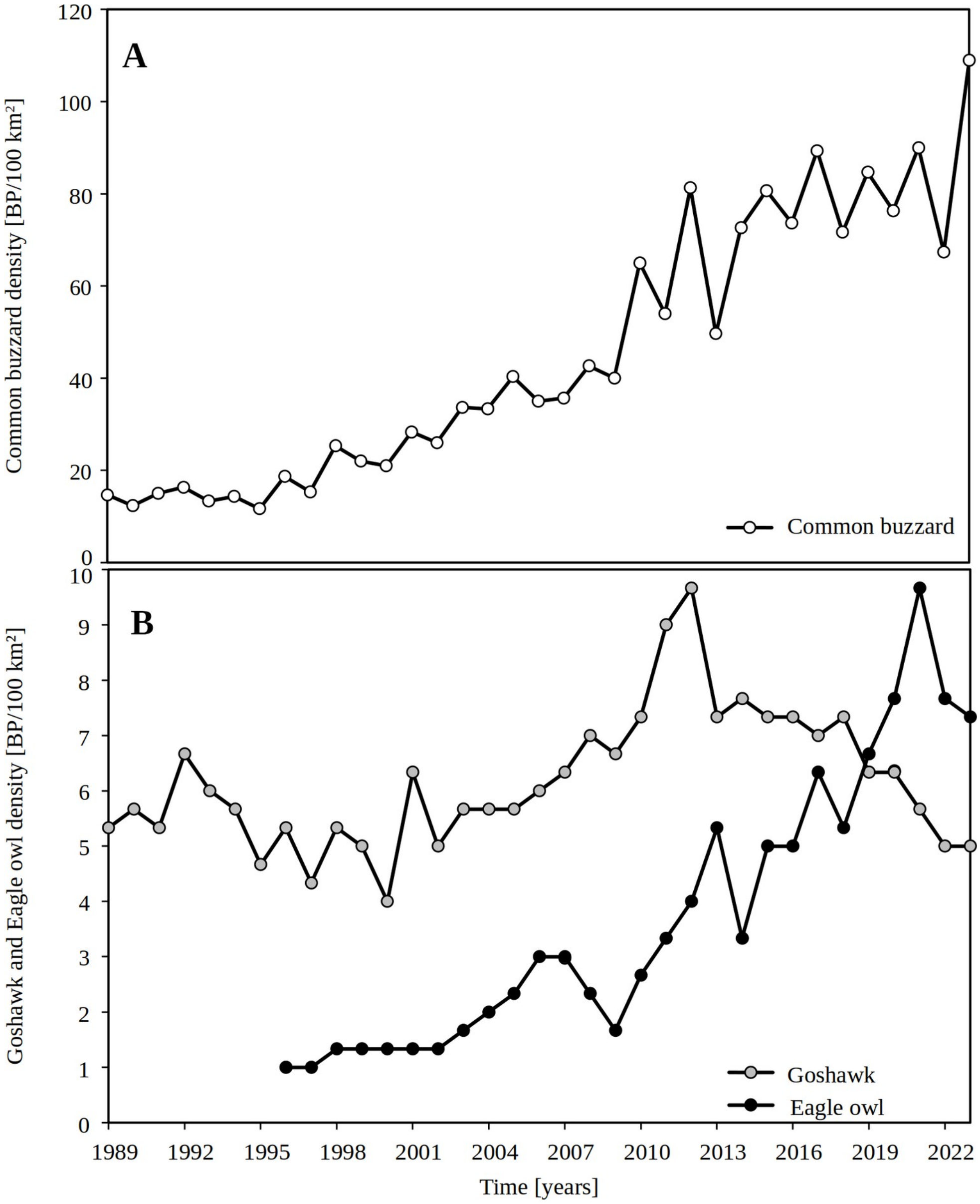

Fig. 1 Population dynamics of common buzzards (A), northern goshawks and eagle owls (B) depicted by the number of breeding attempts in our study area since 1989. Buzzards and eagle owls increased a lot in breeding pairs, goshawks declined on a high level during the last years.

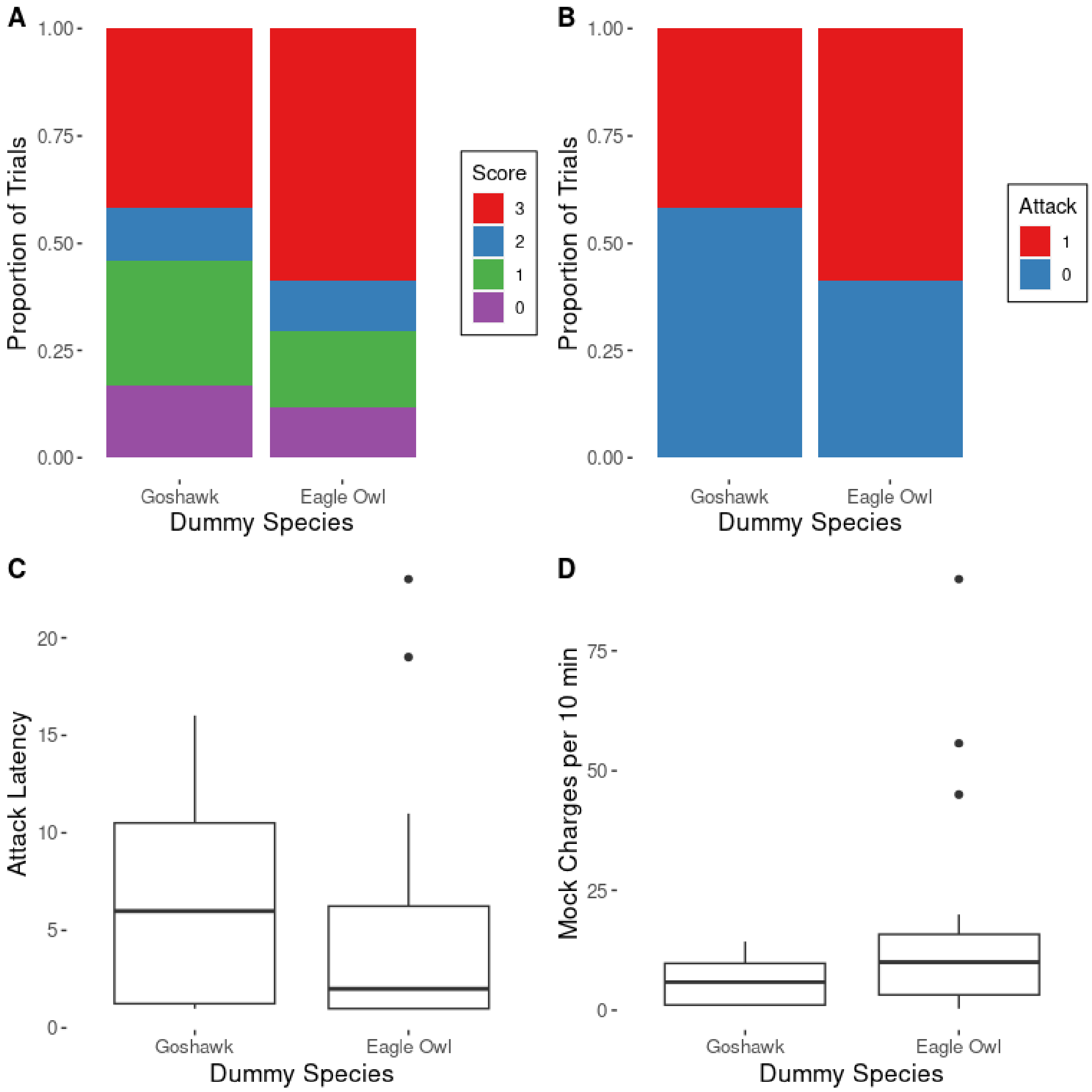

Fig. 2 Reactions of common buzzards towards eagle owl (*Bubo*) or goshawk (*Accipiter*) dummies. Although not completely similar, aggression score (A), proportion of direct attacks (B), attack latency (C) and number of mock charges per trial (D) showed no significant difference between the treatments.

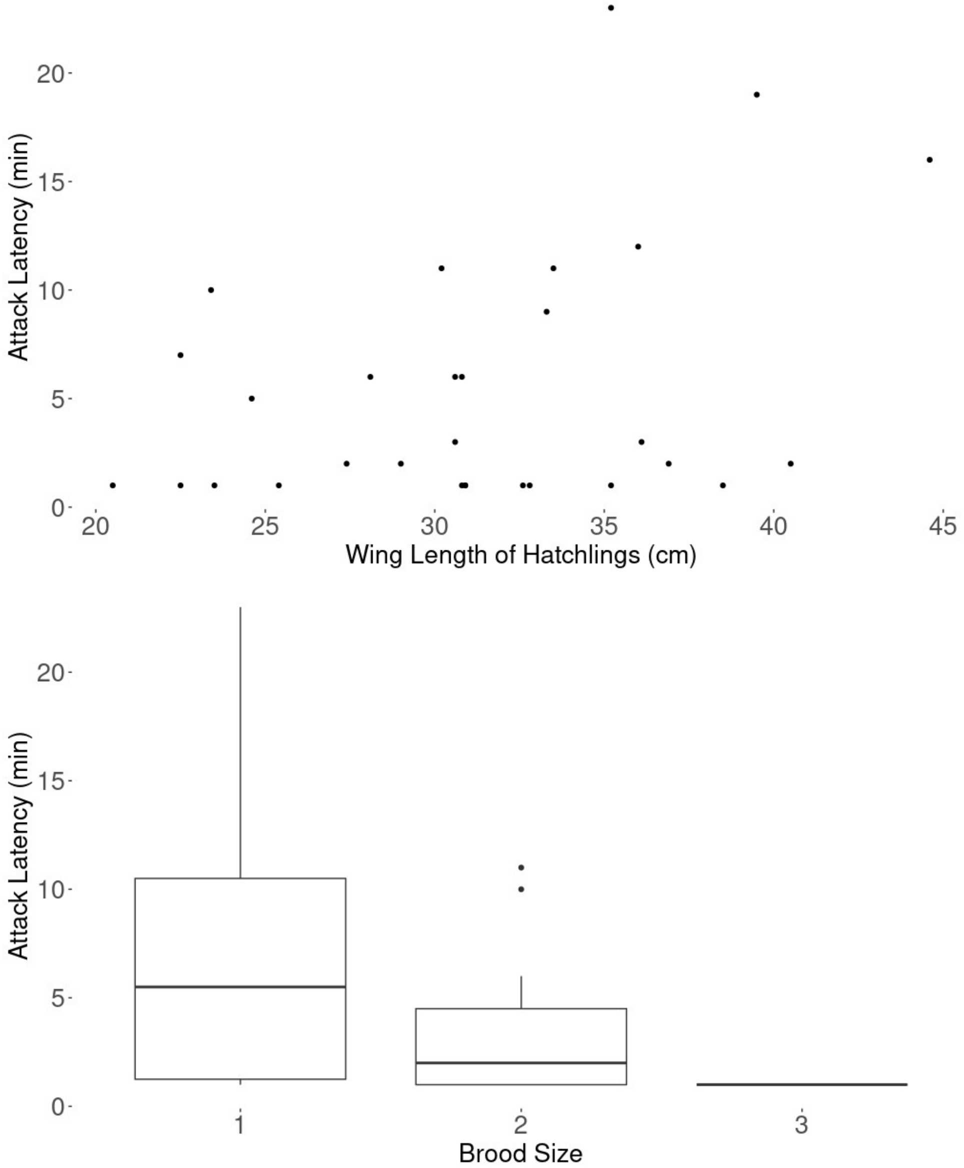

Fig. 3 Association of wing length of hatchlings (top) and brood size (bottom) on attack latency of parent buzzards. Buzzards with more and younger offspring attacked predator dummies faster after detection.

Tables

Table 1 Behaviors measured and methods used to estimate aggressiveness against dummies

Observed Behavior	**Method**	**Further Explanation**
Aggression in general	Scoring aggressive behavior against the dummy (0-3) in a 30 min trial	0: No apparent reaction 1: Circling and calling 2: Mock charges 3: Physical attacks
Physical attacks	Counting trials with and without physical attacks	Attack ratio (amount of trials with attacks)
Latency of attacks	Measuring the time during a trial until a physical attack	Measured in minutes
Number of mock charges	Counting the mock charges	Number of mock charges were corrected for trial length

Table 2 Summary of all test results of our main hypothesis. The Brunner-Munzel test checks if the effect estimator (± the confidence interval) is bigger or smaller than 0.5. A bigger value than 0.5 indicates that the values in the eagle owl group are larger than the data in the goshawk group and vice versa. At the used confidence level (95%), no difference could be detected in all observed behaviors

Dependent variable	n_{EO} [(1)]	n_{NG} [(2)]	Effect estimator	Standard error	T value	Lower CI	Upper CI	p value
Score	34	24	0.5919	0.0714	1.2877	0.4485	0.7353	0.2039
Attack	34	24	0.5858	0.0669	1.2821	0.4514	0.7202	0.2058
Latency	20	10	0.4	0.1143	-0.875	0.1588	0.6412	0.3938
No. Mocks	19	8	0.6678	0.1089	1.5406	0.4412	0.8944	0.1385

(1) n_{EO} = eagle owl dummy sample size. (2) n_{NG} = goshawk dummy sample size.

Table 3 Results of the CLMs for the most likely predictors of aggression score, ranked by AICc score. The model with the lowest AICc is the most parsimonious, which appeared to be the null model (K = number of parameters in the model)

Model parameters	AICc	ΔAICc	AICc Weight	Cumulative weight	K
1. Null model	146.18	0.00	0.14	0.14	3
2. Wing length	146.21	0.03	0.14	0.28	4
3. Wing length + brood size	146.36	0.18	0.13	0.41	5
4. Brood size	147.06	0.88	0.09	0.50	4

Table 4 Results of the GLMs (binomial distribution) for the most likely predictors of physical attacks, ranked by AICc score. The model with the lowest AICc is the most parsimonious, which included wing length and brood size, but did not provide a big difference to the null model (K = number of parameters in the model)

Model parameters	**AICc**	**ΔAICc**	**AICc Weight**	**Cumulative weight**	**K**
1. Wing length + brood size	81.56	0.00	0.18	0.18	3
2. Wing length	82.26	0.71	0.12	0.30	2
3. Null model	82.41	0.85	0.12	0.42	1
4. Brood size	82.65	1.09	0.10	0.52	2

Table 5 Results of the GLMs (Gamma distribution) for the most likely predictors of attack latency, ranked by AICc score. The model with the lowest AICc is the most parsimonious, which included wing length and brood size. That model as well as the models including only each of these variables proved to have AICc values small enough to be distinctively different from the null model (K = number of parameters in the model)

Model parameters	**AICc**	**ΔAICc**	**AICc Weight**	**Cumulative weight**	**K**
1. Wing length + brood size	165.05	0.00	0.25	0.25	4
2. Wing length	165.23	0.19	0.23	0.48	3
3. Brood size	165.41	0.36	0.21	0.69	3
4. Brood size + NND	167.23	2.19	0.08	0.77	4
5. Null model	167.44	2.39	0.08	0.85	2

Table 6 Results of the GLMs (negative binomial distribution) for the most likely predictors of number of mock charges, ranked by increasing AICc score. The model with the lowest AICc is the most parsimonious, which appeared to be the null model (K = number of parameters in the model)

Model parameters	**AICc**	**ΔAICc**	**AICc Weight**	**Cumulative weight**	**K**
1. Null model	246.03	0.00	0.21	0.21	2
2. NND	247.36	1.33	0.11	0.32	3
3. Brood size	247.38	1.35	0.11	0.43	3
4. Parental response	247.60	1.57	0.10	0.53	3

638 **Literature**

Bijlsma R. 1999. Geslachtsdeterminatie van nestjonge Buizerds *Buteo buteo*. Limosa. 72:1-10.

Boerner M, Krüger O. 2009. Aggression and fitness differences between plumage morphs in the common buzzard (*Buteo buteo*). Behav Ecol. 20(1):180–185. doi:10.1093/beheco/arn132.

Björklund H, Santangeli A, Blanchet FG, Huitu O, Lehtoranta H, Lindén H, Valkama J, Laaksonen T. 2016. Intraguild predation and competition impacts on a subordinate predator. Oecologia. 181:257-269. doi:10.1007/s00442-015-3523-z

Brust V, Wuerz Y, Krüger O. 2013. Behavioural Flexibility and Personality in Zebra Finches. Ethology. 119(7):559–569. doi:10.1111/eth.12095.

Caro T. 2005. Antipredator Defenses in Birds and Mammals. Chicago: University of Chicago Press.

Chakarov N, Krüger O. 2010. Mesopredator Release by an Emergent Superpredator: A Natural Experiment of Predation in a Three Level Guild. PLoS ONE. 5(12):8.

Chesson P. 2000. General Theory of Competitive Coexistence in Spatially-Varying Environments. Theor Popul Biol. 58(3):211–237. doi:10.1006/tpbi.2000.1486.

Chesson P, Huntly N. 1997. The Roles of Harsh and Fluctuating Conditions in the Dynamics of Ecological Communities. Am Nat. 150(5):519–553. doi:10.1086/286080.

Christensen RHB. 2022. ordinal—Regression Models for Ordinal Data. R package version 2022.11-16. https://CRAN.R-project.org/package=ordinal.

Curio E. 1987. Animal decision-making and the ‘Concorde fallacy’. Trends Ecol Evol. 2(6):148–152. doi:10.1016/0169-5347(87)90064-4.

Curio E, Klump G, Regelmann K. 1983. An anti-predator response in the great tit (*Parus major*): Is it tuned to predator risk? Oecologia. 60(1):83–88. doi:10.1007/BF00379324.

Fuchs R, Veselý P, Nácarová J. 2019. Predator Recognition in Birds: The Use of Key Features. Cham: Springer International Publishing (SpringerBriefs in Animal Sciences). doi:10.1007/978-3-030-12404-5.

Griesser M. 2009. Mobbing calls signal predator category in a kin group-living bird species. Proc R Soc B. 276(1669):2887–2892.

Holt RD, Polis GA. 1997. A Theoretical Framework for Intraguild Predation. Am Nat. 149(4):745–764. doi:10.1086/286018.

Ibáñez-Álamo JD, Magrath RD, Oteyza JC, Chalfoun AD, Haff TM, Schmidt KA, Thomson RL, Martin TE. 2015. Nest predation research: recent findings and future perspectives. J Ornithol. 156(1):247–262. doi:10.1007/s10336-015-1207-4.

Kappers EF, de Vries C, Alberda A, Forstmeier W, Both C, Kempenaers B. 2018. Inheritance patterns of plumage coloration in common buzzards *Buteo buteo* do not support a one-locus two-allele model. Biol Lett. 14(4):20180007. doi:10.1098/rsbl.2018.0007.

Kikuchi DW, Allen WL, Arbuckle K, Aubier TG, Briolat ES, Burdfield-Steel ER, Cheney KL, Daňková K, Elias M, Hämäläinen L, et al. 2023. The evolution and ecology of multiple antipredator defences. J Evol Biol. 36(7):975–991. doi:10.1111/jeb.14192.

Konietschke F, Friedrich S, Brunner E, Pauly M. 2022. rankFD: Rank-Based Tests for General Factorial Designs. https://CRAN.R-project.org/package=rankFD.

Krüger O. 2002a. Analysis of nest occupancy and nest reproduction in two sympatric raptors: common buzzard *Buteo buteo* and goshawk *Accipiter gentilis*. Ecography. 25(5):523–532. doi:10.1034/j.1600-0587.2002.250502.x.

Krüger O. 2002b. Interactions between common buzzard *Buteo buteo* and goshawk *Accipiter gentilis* : trade-offs revealed by a field experiment. Oikos. 96(3):441–452. doi:10.1034/j.1600-0706.2002.960306.x.

Krüger O, Lindström J. 2001. Lifetime reproductive success in common buzzard, *Buteo buteo*: from individual variation to population demography. Oikos. 93(2):260–273. doi:10.1034/j.1600-0706.2001.930209.x.

Kullberg C. 1998. Spatial niche dynamics under predation risk in the willow tit *Parus montanus*. J Avian Biol. 29(3):235–240.

Li X, Klauschies T, Yang W, Yang Z, Gaedke U. 2023. Trait adaptation enhances species coexistence and reduces bistability in an intraguild predation module. Ecol Evol. 13(1):e9749. doi:10.1002/ece3.9749.

Lima SL. 1998. Stress and Decision Making under the Risk of Predation: Recent Developments from Behavioral, Reproductive, and Ecological Perspectives. In: Advances in the Study of Behavior. Vol. 27. Elsevier. p. 215–290.

Lourenço R, Delgado M del M, Campioni L, Goytre F, Rabaça JE, Korpimäki E, Penteriani V. 2018. Why do top predators engage in superpredation? From an empirical scenario to a theoretical framework. Oikos. 127(11):1563–1574. doi:10.1111/oik.05118.

Lourenço R, Penteriani V, Delgado M del M, Marchi-Bartolozzi M, Rabaça JE. 2011. Kill before being killed: an experimental approach supports the predator-removal hypothesis as a determinant of intraguild predation in top predators. Behav Ecol Sociobiol. 65(9):1709–1714. doi:10.1007/s00265-011-1178-2.

Lourenço RF, Rabaça JE. 2006. Intraguild Predation by Eagle Owls in Europe. Airo. 16:63–68.

Mangiafico S. 2024. rcompanion: Functions to Support Extension Education Program Evaluation. https://cran.r-project.org/package=rcompanion

Martin GR. 1986. Sensory capacities and the nocturnal habit of owls (Strigiformes). Ibis. 128(2):266–277. doi:10.1111/j.1474-919X.1986.tb02674.x.

Martin TE, Martin PR, Olson CR, Heidinger BJ, Fontaine JJ. 2000. Parental Care and Clutch Sizes in North and South American Birds. Science. 287(5457):1482–1485. doi:10.1126/science.287.5457.1482.

Mazerolle MJ. 2023. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). https://cran.r-project.org/package=AICcmodavg.

McPeek MA. 2017. Evolutionary Community Ecology, Volume 58. Princeton: Princeton University Press.

Mebs T, Schmidt D. 2014. Die Greifvögel Europas, Nordafrikas, Vorderasiens. Stuttgart: Kosmos.

Merling de Chapa M, Courtiol A, Engler M, Giese L, Rutz C, Lakermann M, Müskens G, Horst Y, Zollinger R, Wirth H, et al. 2020. Phantom of the forest or successful citizen? Analysing how Northern Goshawks (*Accipiter gentilis*) cope with the urban environment. R Soc Open Sci. 7:201356. doi:10.1098/rsos.201356.

Mittelbach GG, McGill BJ. 2019. Community Ecology. Oxford: Oxford University Press.

Montgomerie RD, Weatherhead PJ. 1988. Risks and Rewards of Nest Defence by Parent Birds. Q Rev Biol. 63(2):167–187. doi:10.1086/415838.

Mueller A-K, Chakarov N, Heseker H, Krüger O. 2016. Intraguild predation leads to cascading effects on habitat choice, behaviour and reproductive performance. J Anim Ecol. 85(3):774–784. doi:10.1111/1365-2656.12493.

Polis GA, Myers CA, Holt RD. 1989. The Ecology and Evolution of Intraguild Predation: Potential Competitors That Eat Each Other. Annu Rev Ecol Syst. 20(1):297–330. doi:10.1146/annurev.es.20.110189.001501.

Potier S, Mitkus M, Kelber A. 2020. Visual adaptations of diurnal and nocturnal raptors. Semin Cell Dev Biol. 106:116–126. doi:10.1016/j.semcdb.2020.05.004.

R Core Team. 2021. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Ripple WJ, Beschta RL, Fortin JK, Robbins CT. 2014. Trophic cascades from wolves to grizzly bears in Yellowstone. J Anim Ecol. 83(1):223–233. doi:10.1111/1365-2656.12123.

Salazar SM, Hlebowicz K, Komdeur J, Korsten P. 2023. Repeatable parental risk taking across manipulated levels of predation threat: no individual variation in plasticity. Anim Behav. 196:127-149. doi:10.1016/j.anbehav.2022.12.003.

Scherzinger W, Mebs T. 2020. Die Eulen Europas: Biologie, Kennzeichen, Bestände. Stuttgart: Kosmos.

Schutten G-J, Chan C, Leeper TJ, Steuer D. 2023. readODS: Read and Write ODS Files. https://CRAN.R-project.org/package=readODS.

Schwarz JFL, DeRango EJ, Zenth F, Kalberer S, Hoffman JI, Mews S, Piedrahita P, Trillmich F, Páez-Rosas D, Thiboult A, et al. 2022. A stable foraging polymorphism buffers Galápagos sea lions against environmental change. Curr Biol. 32(7):1623-1628.e3. doi:10.1016/j.cub.2022.02.007.

Sergio F, Hiraldo F. 2008. Intraguild predation in raptor assemblages: A review. Ibis. 150:132-145.

Sergio F, Marchesi L, Pedrini P. 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. J Anim Ecol. 72(2):232–245. doi:10.1046/j.1365-2656.2003.00693.x.

Sieving KE, Hetrick SA, Avery ML. 2010. The versatility of graded acoustic measures in classification of predation threats by the tufted titmouse *Baeolophus bicolor*: exploring a mixed framework for threat communication. Oikos. 119(2):264–276. doi:10.1111/j.1600-0706.2009.17682.x.

Sousa WP. 1979. Disturbance in Marine Intertidal Boulder Fields: The Nonequilibrium Maintenance of Species Diversity. Ecology. 60(6):1225–1239. doi:10.2307/1936969.

Svagelj WS, Magdalena Trivellini M, Quintana F. 2012. Parental Investment Theory and Nest Defence by Imperial Shags: Effects of Offspring Number, Offspring Age, Laying Date and Parent Sex. Ethology. 118(3):251–259. doi:10.1111/j.1439-0310.2011.02003.x.

Terraube J, Bretagnolle V. 2018. Top-down limitation of mesopredators by avian top predators: a call for research on cascading effects at the community and ecosystem scale. Ibis. 160(3):693–702. doi:10.1111/ibi.12581.

Torchiano M. 2020. effsize: Efficient Effect Size Computation. https://cran.r-project.org/package=effsize

Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. Fourth. New York: Springer. https://www.stats.ox.ac.uk/pub/MASS4/.

Walls S, Kenward R. 2020. The Common Buzzard. London: Bloomsbury Publishing.

Wickham H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. https://ggplot2.tidyverse.org.