JOURNAL OF
AVIAN BIOLOGY

Research article

Experimental comparison of defence behaviour against different avian top predators in an intraguild prey

Kai-Philipp Gladow, Marla Jablonski, Nayden Chakarov and Oliver Krüger

Department of Animal Behaviour, Bielefeld University, Bielefeld, Germany

Correspondence: Kai-Philipp Gladow (kai-philipp.gladow@uni-bielefeld.de)

Journal of Avian Biology
2025: e03495
doi: 10.1002/jav.03495
Subject Editor: Júlio M. M. Neto
Editor-in-Chief: Jan-Åke Nilsson
Accepted 2 September 2025

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 behaviour of other species. The understanding of such changes is scarce because recordings of behavioural 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 behaviour towards differently sized top predators. Birds adjust the level of nest defence in response to perceived threats. Therefore, we expected birds of prey in intraguild predation systems to show an appropriate level of nest defence against the predator they are faced with, with the highest level shown against the largest 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. Overall, aggression by common buzzards towards eagle owls was greater than towards goshawks, but effect sizes were small and had relatively large confidence intervals. We therefore conclude that the largest predator and the second-largest predator provoke similarly high nest defences. This shows that in ecological communities the largest predator and smaller predators may not belong to different categories from the viewpoint of intraguild prey. Different top predators might be perceived as comparable threats.

Keywords: birds of prey, defence behaviour, eagle owl, intraguild predation, top predator

Introduction

A central task of community ecology is to identify the species, traits and behaviours 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

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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 behaviour. This is unfortunate as the behavioural 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, 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 behaviours like defence strategies, activity levels, or search for hiding locations play important roles in predator–prey interactions and constitute always the first line of defence against a predator (Kikuchi et al. 2023, Salazar et al. 2023). Because of their short-lived nature and immediacy, the study of these behaviours is often much more difficult than documenting effects further down the line such as reproduction, survival or growth. Nonetheless, behaviour 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). These behavioural adjustments can be understood in the context of parental investment theory (Montgomerie and Weatherhead 1988), which predicts that parental effort and risk-taking should increase with the value of current offspring to future reproductive success. For instance, latency to attack a predator may decrease as nestling age or number increase – consistent with the idea that the payoff for defending older or more numerous offspring outweighs the risks to the parent (Caro 2005, Svagelj et al. 2012). This framework helps explain variation in nest defence behaviour as a flexible strategy optimized according to the reproductive value of the brood (Lima 1998).

Asymmetrical IGP systems are typically size-based, meaning that larger intraguild (IG) predators exert higher predatory pressure on IG prey (Polis and Holt 1992, Mueller et al. 2016). Thus, in a complex and asymmetrical IGP system, an IG prey (low rank mesopredator) can be expected to adjust its level of aggression according to the IG predator's size. We tested this key prediction of prey defence 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 (Krüger 2002a, 2002b, Boerner and Krüger 2009, Chakarov and Krüger 2010, 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*, as eagle owls predate on both these species (Chakarov and Krüger 2010, Mueller et al. 2016). Eagle owls, goshawks, and buzzards also compete for nesting sites as well as for food (Krüger 2002a, Mebs and Schmidt 2014, Mueller et al. 2016), thus matching the definition of an intraguild predation system (Polis et al. 1989). Previous studies have measured the aggressive response of common buzzards towards eagle owls, showing influences of parental traits like sex or colour morph (Boerner and Krüger 2009), higher aggression against eagle owls compared to tawny owls (Lourenço et al. 2011), and increased aggression after eagle owl re-introduction (Mueller et al. 2016). Towards other intraguild predators (e.g. northern goshawks; Krüger 2002b), less aggressive responses were found in the past. These findings suggest that defence behaviour against eagle owls should be more prominent than against other predators. However, this has never been tested simultaneously.

To assess the impact of different intraguild predators on the behavioural response of a mesopredator, we carried out a direct comparison. The number and dynamics of breeding sites of buzzards, goshawks and eagle owls were counted in the study area since 1989 to illustrate the probability of behavioural interactions. Therefore, we tested the nest defence behaviour of common buzzards against eagle owls in comparison to northern goshawks. In goshawks, especially the larger females are capable of killing both young and adult buzzards (Björklund et al. 2016), although predation on nestlings is considerably more often reported. The goshawk was the single 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). Eagle owls, both male and female, are bigger, outcompete and prey even upon goshawks as well as adult and juvenile buzzards (Chakarov and Krüger 2010, Mueller et al. 2016) and hence should be perceived as a more dangerous threat by buzzards (Polis and Holt 1992, Ibáñez-Álamo et al. 2015). Eagle owls often attack at dusk and night when also adult buzzards are less able to defend themselves, and can therefore be perceived as a greater danger to adults and offspring (Penteriani and Delgado 2019, Walls and Kenward 2020). In a study by Sergio et al. (2003), eagle owls have been shown to reduce reproductive success in black kites in a 1.5 km radius around their nests, and similar negative effects are likely for other IG species. 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 hypothesize that buzzards should show a higher level of aggression when defending their nest against eagle owls in comparison to goshawks.

Material and methods

Study area and species

The study area is located west of the city of Bielefeld in North Rhine-Westphalia and Lower Saxony, Germany (52°3'36''N, 8°18'0''E). It measures 300 km^2 in size and includes three different natural regions: the largest part in the north consists of a hilly terrain with mostly rural landscape and patches of deciduous forest (mainly European beech *Fagus sylvatica*); the Teutoburg Forest in the center is a low mountain range covered by 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 (Krüger 2002a, Mueller et al. 2016). The most important characteristics of common buzzards, goshawks and eagle owls are listed in Table 1. Other raptor species sighted but usually not investigated are sparrowhawks *Accipiter nisus*, black kites *Milvus migrans*, western marsh harriers *Circus aeruginosus*, honey buzzards *Pernis apivorus*, barn owls *Tyto alba*, tawny owls *Strix aluco*, long-eared owls *Asio otus*, little owls *Athene noctua*, Eurasian hobbies *Falco subbuteo*, peregrines *Falco peregrinus*, and kestrels *Falco tinnunculus*. Except sparrowhawks, barn owls, tawny owls, and kestrels, these species are only present occasionally, with very few breeding pairs.

Monitoring of breeding attempts

Since 1989, all breeding attempts of birds of prey, including common buzzards and northern goshawks have been mapped for the whole study area (Krüger and Lindström 2001). Breeding attempts were identified through extensive mapping of all forests for active nests. 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.

Aggression experiments – general aspects

Nest mapping for the presented experiment 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 those 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 active nests in our area, therefore our sample was representative of the study population. In the end, the chicks were between 25 and 60 days old.

Earlier studies claiming to test nest defence behaviour in buzzards used the same methods (Boerner and Krüger 2009), measuring parental reactions to eagle owl models. Because of this, we expected that our procedure tested nest defence too, rather than only defence behaviour in general. However, we cannot rule out that we did not test nest defence explicitly but rather general aggression against predators or territory intruders, especially since the models were not placed directly at the nest but at a distance of between 50 and 80 m, allowing a clear sight of the models.

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 with juvenile plumage, both taxidermic models). The plastic eagle owl was painted and equipped with feathers to resemble a real eagle owl as closely as possible. No playbacks of eagle owls, goshawks or buzzards were used to additionally attract focal common buzzards. The experiment did not represent any risk to the buzzard individuals involved.

For our research question, the goshawk treatment (long-present IG predator) served as the control setting for the eagle owl treatment (larger IG predator). We did not use other stimuli as a general baseline control (e.g. conspecifics, another

Table 1. Characteristics of the study species taken from Mebs and Schmidt (2014) and Scherzinger and Mebs (2020).

Species	Common buzzard *Buteo buteo*	Northern goshawk *Accipiter gentilis*	Eurasian eagle owl *Bubo bubo*
Body weight (g)	800–1000	900–1300 (♀) 600–900 (♂)	2200–3200 (♀) 1600–2100 (♂)
Wing span (cm)	115–140	115 (♀) 100 (♂)	168 (♀) 157 (♂)
Activity times	diurnal	diurnal	nocturnal/crepuscular
Main food sources	small mammals (mainly field voles), young birds, roadkill, invertebrates	birds (mainly pigeons), mammals (mainly rabbits)	mammals (from mice to hares), birds (pigeons, crows, birds of prey)

mesopredator or a harmless bird). This was done because potential aggression against these species could arise from very different reasons than from nest defence, such as competition for food, mating, or viewing the stimulus as a prey item, and disentangling these effects is very difficult. Furthermore, it has been shown that buzzards react less intensely to smaller mesopredators like tawny owls (Lourenço et al. 2011).

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 4 June and 8 July 2022, leading to a final sample size of trials at 58 nests (34 times with the eagle owl models and 24 times with the goshawk models). After arrival at a nesting site, we placed one of the dummies on a tripod close to the forest edge in 50–80 m from the buzzard nest and made sure it reached above the surrounding vegetation for visibility. We returned to the car and waited for 30 min to see whether at least one of the adult buzzards would appear in sight, otherwise we moved to the next territory. Buzzard territories are comparatively small and average feeding rates peak during the time of our experiments, but buzzards can go for long foraging trips (Walls and Kenward 2020). Thus, we avoided waiting too long for parental birds by discontinuing a trial after 30 min without a reaction. When a buzzard appeared and had a clear view of the dummy, we started the behavioural observation, which lasted for 30 min. The buzzard's reaction to the dummy was measured by recording the behaviours listed in Table 2. We also recorded the date, time, trial number, territory name, individual nest number, and dummy used (ID and species). Adult buzzards were not caught using our dummies and were not confronted with this or similar procedures before our experiments.

Trials were stopped before reaching the 30 min limit if 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 active eagle owl or goshawk nest, 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 for for hatching date (Bijlsma 1999). The parental response during ringing of the chicks was scored on five different levels (no reaction–fleeing–circling and calling–coming closer than 20 m–attempting a charge on the climber). The number of offspring varied between one and three hatchlings per nest. Distance to the nearest breeding eagle owl pair varied between 0.58 and 4.61 km, and distance to the next breeding goshawk pair varied between 0.11 and 5.57 km. Each buzzard pair included was tested with one dummy species only (eagle owl or goshawk, not both). Consecutive trials were not conducted in neighbouring territories to avoid that the focal birds were influenced by previous trials.

Statistical analysis

For the statistical analysis, we used the open-source software R (www.r-project.org) with the additional packages 'MASS', 'rankFD', 'ordinal', 'AICcmodavg', 'readODS' and 'ggplot2' (Venables and Ripley 2002, Wickham 2016, Christensen 2022, Konietschke et al. 2022, Mazerolle 2023, Schutten et al. 2023). Per trial, we only used the data of the first individual reacting to the dummy, even if two birds were present later during the trial. We performed two-tailed 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 used generalized linear models (GLMs) as well as cumulative link models (CLMs) for further analysis of potential effects on the behaviour. These potential effects were wing length of the oldest offspring, brood size, nearest neighbour distance (NND) to the next breeding predator (eagle owl/goshawk, depending on treatment), and parental response when the nest was climbed to ring the offspring. CLMs were used for models testing effects on the aggression score (ordinal data). In the GLMs, a binomial distribution was assumed when testing for effects on the attack ratio, a Gamma distribution was assumed when testing for effects on the attack latency, and a negative binomial distribution was assumed when testing the effects on the number of mock charges. We decided to use the respective assumptions after visually

Table 2. Behaviours measured and methods used to estimate aggressiveness against dummies.

Observed behaviour	Method	Further explanation	Variable TYPE
Aggression in general	scoring aggressive behaviour against the dummy (0–3) in a 30 min trial	0: no apparent reaction 1: circling and calling 2: mock charges 3: physical attacks	ordinal (rank)
Physical attacks	counting trials with and without physical attacks	attack ratio (no. of trials with attacks)	binomial (yes/no)
Latency of attacks	measuring the time during a trial until a physical attack	measured in minutes	continuous
Number of mock charges	counting the mock charges	number of mock charges were corrected for trial length	continuous (count)

inspecting the data distribution and considering the level of measurement. For model selection, we compared the parsimony of models containing different variables using their AICc (when models had an AICc value that was two values smaller than the AICc of the null model, they were considered more parsimonious).

The Brunner–Munzel test is a non-parametric test that is very robust against large differences in data structure of the two compared samples, such as sample size or distribution equality, and is also very useful if the data has many outliers, as is often the case in ecological or behavioural data (Konietschke et al. 2022). Furthermore, the output provides effect estimates with corresponding confidence intervals for a detailed interpretation of treatment effects. The effect estimator is 0.5 if no difference between the treatments can be detected; the closer it is to zero or one, the greater the difference (Konietschke et al. 2022).

Results

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

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 one breeding pair per 100 km^2 to a maximum of over nine breeding pairs per 100 km^2 (Fig. 1B). In slight contrast, the population dynamics of the goshawk show a stable population size with between five and seven breeding pairs per 100 km^2 (Fig. 1B). The densities of the three species are among the highest reported (common buzzard, eagle owl) or above average for central Europe (goshawk), making frequent behavioural interactions very likely (Mebs and Schmidt 2014, Scherzinger and Mebs 2020).

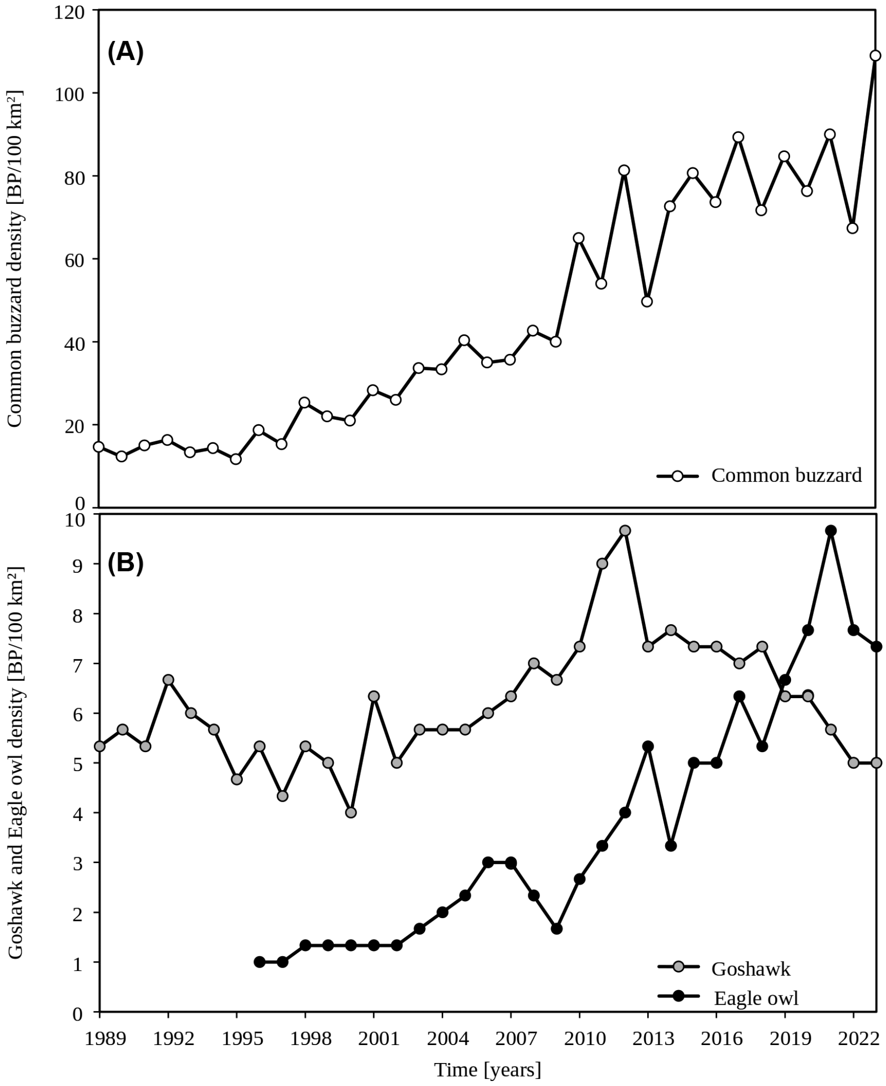

Figure 1. Population dynamics of common buzzards (A), northern goshawks and eagle owls (B) depicted by the number of breeding attempts in the study area since 1989. Buzzards and eagle owl density strongly increased, goshawks population dynamics was not unidirectional over the years.

Descriptive analysis of the behavioural experiments

With the time limit of all chicks having fledged by 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 (Fig. 1).

Out of these 125 territories, 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%). Table 3 shows the reaction of buzzards to the different treatment types in detail.

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 (Brunner–Munzel tests: eagle owl $T = -0.511$, $n_1 = 14$, $n_2 = 20$, $p = 0.613$; goshawk $T = 0.685$, $n_1 = 15$, $n_2 = 9$, $p = 0.500$).

Defence behaviour against two intraguild predators

Overall, we did not find a significant difference between the buzzard reactions towards eagle owls and goshawks (Table 4).

Although the difference between goshawk and eagle owl trials appeared rather large with regard to the proportions of direct attacks and 'circling and calling' responses, our statistical analysis did not show a significant difference, neither for the aggression score overall (Brunner–Munzel test: $T = 1.288$, eagle owl $n = 34$, goshawk $n = 24$, $p = 0.204$), nor for the amount of direct attacks alone (Brunner–Munzel test: $T = 1.282$, eagle owl $n = 34$, goshawk $n = 24$, $p = 0.206$; Fig. 2, Table 4).

Among trials with direct attacks (score = 3), the median attack latency (+ IQR) was 2.5 + 7.5 min. Eagle owl dummies seemed to be attacked faster (2.0 + 5.25 min) than goshawk dummies (6.0 + 9.25 min), but there was no significant difference between the groups (Brunner–Munzel test: $T = -0.875$, eagle owl $n = 20$, goshawk $n = 10$, $p = 0.394$; Fig. 2).

The median number of mock charges per 10 min with eagle owls was 10 + 12.67, with goshawks 5.83 + 8.67. Similar to the other variables, we did not find a significant difference between the treatments (Brunner–Munzel test: $T = 1.541$, eagle owl $n = 19$, goshawk $n = 8$, $p = 0.139$; Fig. 2). Interestingly, buzzards exerted mock charges in a greater proportion of trials including eagle owl dummies than goshawk dummies (55.9 versus 33.3%).

To have more detailed information about the treatment effects, we also observed the effect sizes (estimators) of our samples. For all four defence behaviours, we found a small effect for higher aggression towards eagle owl dummies, deviating between 0.0858 and 0.1678 from 0.5 (Table 4). However, the confidence intervals for all four traits were very broad as well (Table 4), which prohibits a statement on treatment effects. Since this is to our knowledge the first study comparing impact of different predators on intraguild prey in an experimental setup, comparisons with effect sizes of other studies is not possible.

Other factors influencing buzzard nest defence

In most of our linear models, other possible effects including dummy species had only a minor explanatory power for the defence behaviour. Age (measured by wing length) and number of offspring in the current brood were often 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 (Table 5, 6, 8). The only exception were effects on the attack latency where the best model included both age and number of offspring and had an ΔAIC greater than 2 compared to the null model (Table 7). Buzzards with more and younger hatchlings attacked the dummies faster (Table 7, Fig. 3).

Discussion

We found that in an intraguild predation context a subordinate mesopredator exhibits similar defence behaviour against two intraguild predators of different size. This differs from our expectations based on literature and theory dealing with 1) top predator impact on communities, 2) prey behaviour, and 3) previous experiments with raptors (Polis et al. 1989, Holt and Polis 1997, Lourenço et al. 2011, Mueller et al. 2016, Salazar et al. 2023, Fišer et al. 2025). This leads to several implications which we discuss here.

We found no significant difference between the intensity of nest defence behaviour 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 analysing 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 (2002b). There, buzzards

Table 3. Reactions of buzzards to the different treatment types (eagle owl or goshawk dummy). Numbers of trials with corresponding reactions are listed together with the percentage of trials per treatment. Score levels are shown in parenthesis after the behavioural category.

Treatment type	Total no. of trials	Direct attacks (3)	Mock charges (2)	Circling and calling (1)	No reaction (0)
Eagle owl	34 (100%)	20 (58.8%)	4 (11.8%)	6 (17.6%)	4 (11.8%)
Goshawk	24 (100%)	10 (41.7%)	3 (12.5%)	7 (29.2%)	4 (16.7%)

Table 4. Summary of all test results of our main hypothesis. The Brunner–Munzel test checks if the effect estimator (± the confidence interval) is greater or lesser than 0.5. A greater 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 (CI 95%), no significant difference could be detected in all observed behaviours. [a]n_{EO} = eagle owl dummy sample size; [b]n_{NG} = goshawk dummy sample size.

Dependent variable	n_{EO}[a]	n_{NG}[b]	Effect estimator	SE	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
Swoop	34	24	0.5821	0.0654	1.2563	0.4506	0.7136	0.2153
Attack 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

showed only very little aggression against goshawk dummies (only 1 out of 14 pairs performed a physical attack; possible reasons are considered further below).

Population demographics

The population densities observed in our study area – over 100 common buzzards pairs and between five and seven goshawks pairs per 100 km² – are among the highest densities reported for these species (Squires and Kennedy 2006, Walls and Kenward 2020). The population density for eagle owls – up to nine pairs per 100 km² – reflects at least a rarely observed high density (Penteriani and Delgado 2019). These densities make behavioural interactions of common buzzards with both eagle owls and goshawks within our study area very likely. Nolte (1969) estimated in his study, conducted in a neighbouring and partly overlapping area of the same size (300 km²), a maximum of 314 breeding pairs of common buzzards under ideal conditions. This number is now surpassed for our area; future monitoring will show if the carrying capacity has been reached.

Implications on intraguild predation theory

Our results question some predictions made by theoretical concepts about intraguild predation and the importance of a single top predator species in these models (Polis et al. 1989, Holt and Polis 1997). In general, predation is often

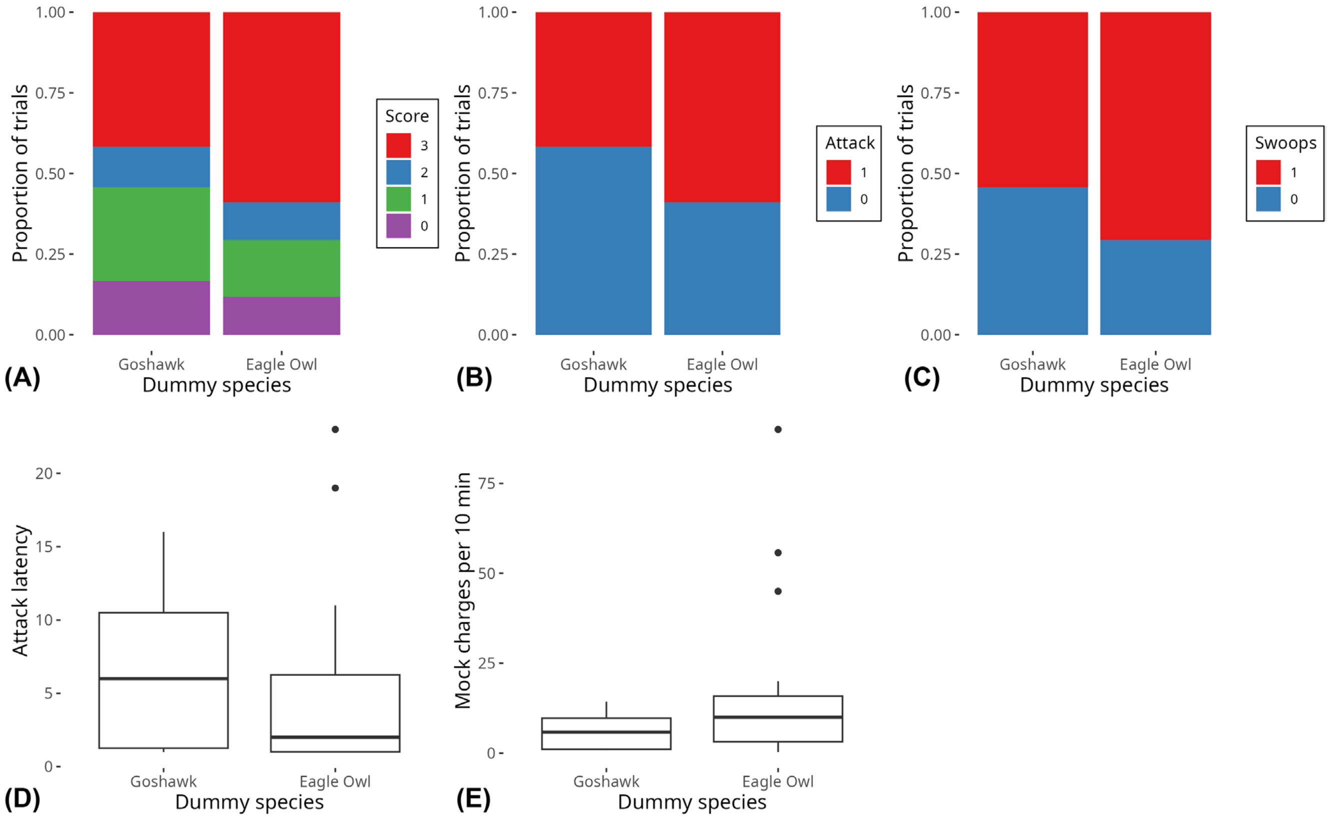

Figure 2. Reactions of common buzzards towards eagle owl or goshawk dummies displayed as stacked barplots (A–C) and boxplots showing median, 50% quartiles, 95% range and outliers (D–E). Although not completely similar, aggression score (A), proportion of direct attacks (B), proportion of trials with swoops (mock charges and real attacks; C), attack latency (D) and number of mock charges per trial (E) showed no significant difference between the treatments.

Table 5. 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

considered a factor with strong influence on community structure, hence the importance of top predators for food webs (Lourenço et al. 2018, Mittelbach and McGill 2019). In many publications and theoretical models, 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 (Holt and Polis 1997, Lourenço et al. 2018, Terraube and Bretagnolle 2018). To our knowledge, this is the first study directly comparing the effect of the largest top predator on defence behaviour with the effect of the second-largest top predator in an IGP setting. In other such experiments, either no comparison was done or the comparison was on an IG prey (Lourenço et al. 2011, Mueller et al. 2016). Our results suggest that although a predator species itself can be preyed upon by larger predatory species, mesopredators may be impacted similarly by higher-ranked predators, even if these are different in size. This fits to previous results showing high ecological similarity between goshawks and eagle owls with high overlap in breeding habitat characteristics, with the eagle owl, after its recolonization, driving out the goshawk from long-term territories (Chakarov and Krüger 2010, Mueller et al. 2016). The mechanisms of this displacement are still not well understood.

Most IGP models and empirical studies analyse 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 for understanding 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.

Table 6. Results of the GLMs (binomial distribution) for the most likely predictors of physical attacks, ranked by AICc score. 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 7. Results of the GLMs (Gamma distribution) for the most likely predictors of attack latency, ranked by AICc score. K = number of parameters in the model. NND = nearest neighbour distance to the next breeding predator that was used in the respective treatment (eagle owl/goshawk).

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

Implications on defence behaviour and predator recognition

Potential prey species (and individuals) are known to adjust their behavioural defence 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 (Fuchs et al. 2019). Without significant differences in the behaviours against the two predator species and with small effect sizes, it appears that common buzzards do not perceive eagle owls to be more dangerous than female goshawks. This might be due to several reasons. We tested buzzards during their chick-rearing period. Both eagle owls and goshawks serve as effective predators of buzzard nestlings, so even if there was a difference in danger for adult birds, the high danger for the nestlings could lead to a similar nest defence behaviour by their parents. In contrast to adults, nestlings cannot leave the area to avoid predation. Thus, defensive behaviour of buzzard parents might not be regulated by risk for their own survival in the first place, but the risk to their offspring seems to determine more how strongly they react to potential predators, aligning with parental investment theory (Montgomerie and Weatherhead 1988, Caro 2005, Ibáñez-Álamo et al. 2015). Another explanation could arise from the different activity times of eagle owls and goshawks. Whereas goshawks are mostly diurnal raptors, eagle owls mainly hunt during twilight and night and hence have adapted to

Table 8. Results of the GLMs (negative binomial distribution) for the most likely predictors of number of mock charges, ranked by increasing AICc score. K = number of parameters in the model. NND = nearest neighbour distance to the next breeding predator that was used in the respective treatment (eagle owl/goshawk).

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

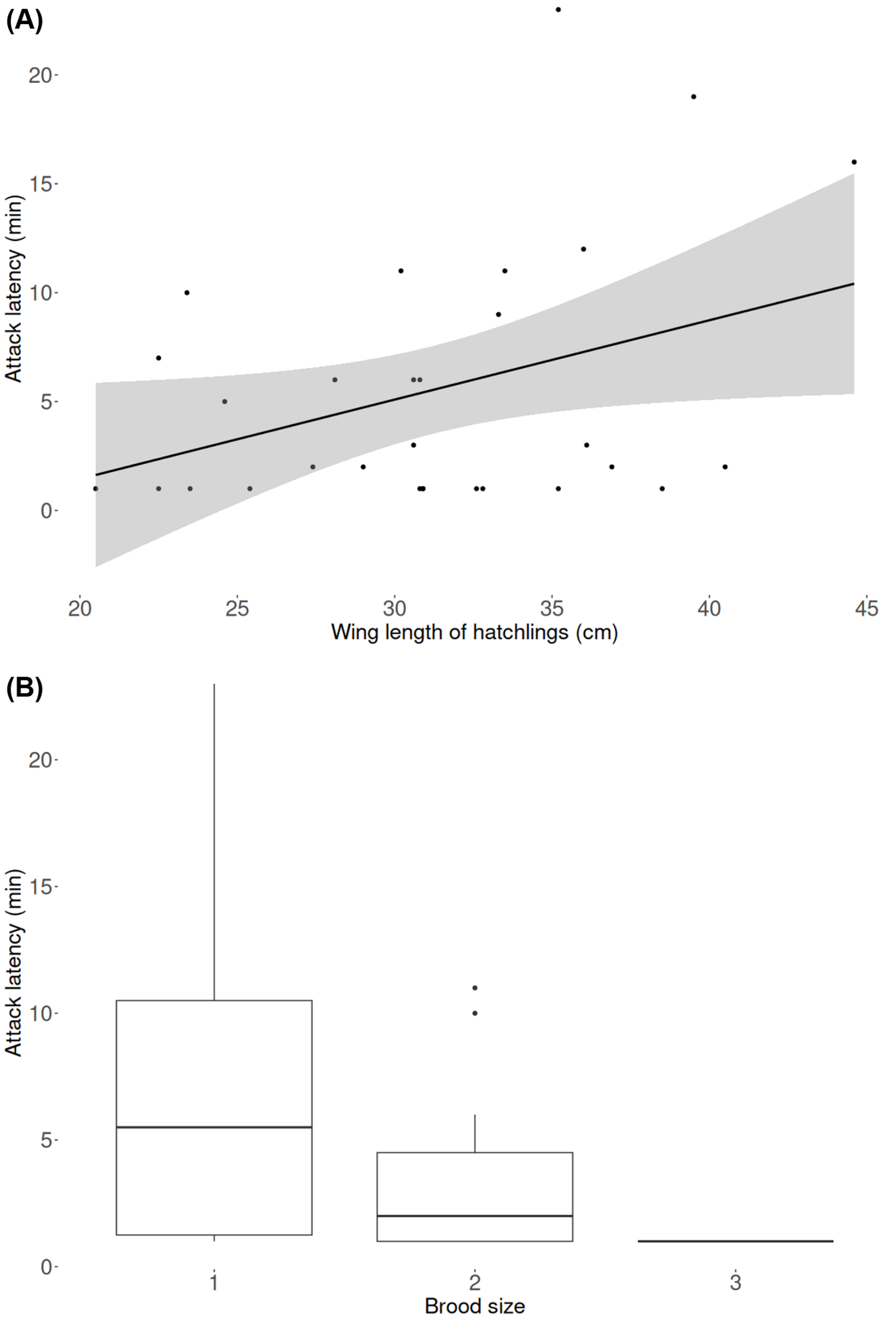

Figure 3. Association of wing length of hatchlings depicted as a scatterplot with a trendline and 95% confidence intervals (A) and brood size depicted using boxplots displaying (B) on attack latency of parent buzzards. Buzzards with more and younger offspring attacked predator dummies faster after detection.

their respective environment (Squires and Kennedy 2006, Penteriani and Delgado 2019, Walls and Kenward 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 may not have been perceived as a greater threat than female 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 (Potier et al. 2020).

Comparison with related studies

Based on earlier aggression experiments with common buzzards, a greater difference in nest defence was expected. Although there have been studies investigating the influence of goshawks on common buzzards (Björklund et al. 2016), only one empirical study analysed direct behavioural reactions of common buzzards to northern goshawks (Krüger 2002b). The observed aggression was very low in contrast to the comparatively high frequency of direct and mock attacks in our study. One possible explanation could lie 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. Krüger (2002b) also used only male goshawk dummies, which are smaller in size (Squires and Kennedy 2006) and therefore potentially less threatening to buzzards. In contrast, we used only female goshawks. Furthermore, Krüger (2002b) used playback calls of goshawks in addition to the visual presence of the dummy. It is a common reaction of prey species to hide away from predators if they are aware of a predator's presence, especially when the predator has not noticed the prey yet (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 and thereby prevent spontaneous reaction. Thus, dummies were placed in the open field to be clearly visible for approaching buzzards. Corresponding tests with this study design modification remain to be done and compared.

Our results, especially the question of (non-)significant differences, could of course be influenced by our sample size, which was as large as possible given the limited time of the breeding season, but still relatively small. The observed effect sizes always indicated a small effect of higher aggressiveness against eagle owls, but with broad confidence intervals. This suggests a rather fine-scaled, probably very variable differentiation between the two treatments by individual buzzards. The choice of partly quite coarse measurements, like an aggression score, might be disadvantageous for such fine-scaled differences.

Hence, to get a better interpretation of our treatment effects in the future, we call upon other researchers working on predator interactions to perform comparable experiments. This may be in the same or other systems, but as long as effect sizes and confidence intervals are provided for comparability, it will help us to understand the generality of such results (Nakagawa and Cuthill 2007).

Other influences on defence behaviour

The possible correlates of defence behaviour 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 defence with more offspring is congruent with theory (Curio 1987, Montgomerie and Weatherhead 1988, Caro 2005, Svagelj et al. 2012). With regard to offspring age, however, a higher nest defence for older chicks was 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. More research, including repeated and longitudinal trials, is needed to decompose and understand different aspects of defence reactions.

We did not find a consistent dependence of reaction intensity on the age of offspring or the already allocated investment. Krüger (2002b) found a correlation between aggression and offspring age for both for conspecifics and goshawk stimuli, but a correlation with offspring number only for 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). A solid number of trials per brood size and across the whole nestling period would be needed to resolve discrepancies between these studies, as well as a measurement of breeding site quality, for example, the number of prey items brought to the nest or the breeding success in the years before.

Conclusion

The different effects that top predators have on the behaviour of potential prey are key to understanding their effects on ecological communities. In this study, we showed that a subordinate mesopredator did not show strong differences in its nest defence behaviour toward two intraguild predators of different size in the community. This suggests that the danger emanated by the largest predator may be perceived similarly by their intraguild prey as the danger of other intraguild predators. Behavioural reactions should be considered more carefully when estimating the impact of certain species on ecological communities. In particular, intraguild predation models and investigations in the wild should consider multiple top predator species influencing their intraguild prey in a similar way.

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. Open Access funding enabled and organized by Projekt DEAL.

Funding – This work was supported by the Friedrich-Ebert-Stiftung (FES) to KPG and the German Research Foundation (DFG; project no. 398434413), as part of the SFB TRR 212 (NC^3; project no. 316099922 and 396780709) to OK and NC.

Conflict of interest – The authors declare no conflict of interest.

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 and editing (equal). **Marla Jablonski**: Conceptualization (supporting); Data curation (supporting); Investigation (equal); Methodology

(supporting); Writing – review and editing (equal). **Nayden Chakarov**: Data curation (supporting); Funding acquisition (equal); Investigation (supporting); Project administration (supporting); Resources (lead); Supervision (equal); Writing – review and editing (equal). **Oliver Krüger**: Conceptualization (supporting); Funding acquisition (equal); Methodology (supporting); Resources (supporting); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Publications at Bielefeld University public repository: https://doi.org/10.4119/unibi/3006466 (Gladow et al. 2025).

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