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Review of inter and intraspecific predation by shorebirds

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Predation is often the most important driver of breeding productivity and population dynamics in birds, with an increasing impact in the currently rapidly changing world. Despite decades of intensive research, our understanding of trophic interactions and food webs is still limited. Although there is good knowledge of regular predators within particular groups of animals, focused overviews of such predator-prey interactions are often lacking. Here, I review predation behaviour by shorebirds: plovers, sandpipers and allies, over the globe – presenting 16 cases of interspecific predation relationships and two cases of intraspecific predation of eggs or chicks, altogether involving 11 species of predators and 13 species of prey. Predator species are usually bigger and more aggressive than prey species. Contrary to the usually anecdotal nature of predation interactions among shorebirds, Ruddy Turnstone (*Arenaria interpres*) and Bristle-thighed Curlew (*Numenius tahitiesis*) can represent a significant threat for other breeding birds in coastal habitats, where high egg depredation rates can be detrimental, causing complete reproduction failure in colonies of gulls and terns. Apart from pointed bill of both species, Bristle-thighed Curlew, uniquely among shorebirds, can use stones for egg opening. Furthermore, turnstones are not perceived as potential predators in gull colonies which render them successful egg predators. This review (i) suggests that even shorebirds, generally perceived as consumers of invertebrate prey, can become vigorous predators of vertebrates including their own kind; (ii) highlights that such behaviour might be overlooked and more common than previously supposed, possibly present in other groups of birds too, extending our knowledge on food web complexity.

1. Introduction

Predation is the most probable fate for a large proportion of organisms upon Earth (Sih *et al.* 1985, Polis *et al.* 1989, Lima & Dill 1990, Barbosa & Castellanos 2005) and a powerful force shaping diverse behavioural, morphological and life-history anti-predatory adaptations (Lima 1998, Caro 2005). Predation has a pivotal influence on reproduction performance in all animals (Skutch 1949,

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Fig. 1. A bigger and more aggressive Black-shouldered Lapwing (*Vanellus novaehollandiae*) (on the left) can predate upon eggs or chicks of Northern Red-breasted Plover (*Charadrius aquilonius*) (on the right) at New Zealand, photographs taken by Vojtěch Kubelka.

Lack 1966, Bailey & Houde 1989), with often direct impacts on whole population dynamics (Evans & Pienkowski 1984, Bennett & Owens 2002, Blackburn *et al.* 2004). Predation can happen among the members of the same clade, but such information is often scattered and rarely reviewed for the whole coherent group of animals (Barbosa & Castellanos 2005), but our better understanding of food webs and predator-prey interactions is even more important now, in rapidly changing word (Tylianakis *et al.* 2008, Gilg *et al.* 2012, Roodbergen *et al.* 2012, Scheffers *et al.* 2016, Kubelka *et al.* 2018).

To fill this scientific knowledge gap, here I review inter and intra specific predation within a distinctive group of birds. Shorebirds (plovers, sandpipers and allies) are generally perceived as predators of invertebrate prey, varying from insects, lumbricids to bivalves (e.g. Colwell 2010, BirdLife International 2018, del Hoyo *et al.* 2018). However, particular occasions suggest that these gentle creatures can purposefully prey on other vertebrates, including eggs of other birds (e.g. Cramp & Simmons 1983, Poole 2015). In this review, I focus on specific cases, when one species of shorebird predates on eggs or chicks of other shorebird species followed by the consumption of the prey.

2. Material and methods

I considered as shorebirds 245 species from 16 families classified into the order Charadriiformes (del Hoyo & Collar 2014, Gill & Donsker 2016, del Hoyo *et al.* 2020). I excluded gulls, terns and auks for the better eco-morphological coherence of the focal species (del Hoyo *et al.* 2020). I searched for suitable information using keywords (species Latin name + "predation") in electronic databases including Web of Science, Searchable Ornithological Research Archive and Google Scholar and reference books (Cramp & Simmons 1983, Urban *et al.* 1986, Marchant & Higgins 1993, del Hoyo *et al.* 1996, Higgins & Davies 1996, Lappo *et al.* 2012, Poole 2015). I either downloaded articles from electronic databases or photocopied the printed version in the ornithological Alexander Library in Oxford (UK).

Additionally, I asked members of International

Wader Study Group for published grey literature and unpublished information concerning predatory interactions among shorebirds. I obtained the average adult body mass for each interacting species from Myhrvold *et al.* (2015) and defined the species as non-aggressive or aggressive against potential predators (actively attacking them) during incubation or chick-rearing period according to Larsen *et al.* (1996) with use of current information (del Hoyo *et al.* 2020) and primary literature for some species.

Situations, when shorebird females were observed just to attack and kill a chick from another family at the border of family foraging ranges in lapwings or godwits (Byrkjedal *et al.* 2000, Teunissen *et al.* 2008) or reported destroying eggs and infanticide among parents in several species of Jacanas (D. A. Jenni in Stephens 1982, Emlen *et al.* 1989, Chen *et al.* 2008) where victims were not consumed, were omitted from this review. The statistical analysis was performed with R ver. 3.3.3 (R Development Core Team 2017) and the test was two-tailed.

3. Results

I obtained 16 cases of interspecific predation relationships and two cases of intraspecific predation among shorebirds, altogether involving 11 species of predators and 13 species of prey over the globe (Fig. 1, Table 1). Regarding all 18 interactions, predator species had on average bigger body mass: 285 g ± 49 (SE) than prey species of shorebirds: 164 g ± 41 (SE) and they differed significantly (paired Wilcoxon signed rank test; $P = 0.007$). In all 18 interactions, predator shorebirds were always regarded as aggressive species against potential predators during breeding (100%), whereas prey shorebirds were defined as aggressive ones only in 44% of cases.

4. Discussion

4.1. Turnstones

Both, Ruddy Turnstone (*Arenaria interpres*) and Black Turnstone (*Arenaria melanocephala*) are well known as opportunistic feeders with very diverse diet, known to contain eggs of small ground-nesting birds (Cramp & Simmons 1983, Handel & Gill 2001). Therefore, it is unsurprising that Ruddy Turnstone is the most common species involved in predation among shorebirds (Table 1). Apart from presented interactions, Ruddy Turnstone is a highly suspected egg predator of Common Ringed Plover (*Charadrius hiaticula*) according to direct observation at Swedish Öland Island (L. Hedh *pers. comm.*). Ruddy Turnstone is known to predate and consume eggs of other water birds, namely several species of terns, gulls or ducks across locations ranging from Palearctic to North America and Pacific islands (Bergman 1946, Crossin & Huber 1970, Parkes *et al.* 1971, Loftin & Sutton 1979, Brearey & Hildén 1985, Farraway *et al.* 1986, Morris & Wiggins 1986, Alberico *et al.* 1991, Olson 1996).

Sometimes it is not just an accidental predation, but turnstones can cause a large nest predation and damage issuing e.g. in the Royal Tern (*Thalasseus maximus*) colony abandonment in Florida (Loftin & Sutton 1979), or depredation of a large proportion of Common Tern (*Sterna hirundo*) nests within a breeding colony in Toronto (Farraway *et al.* 1986), or plunder gulls and terns colonies at Scandinavian islands (Brearey & Hildén 1985). Nest depredation on Gray-backed Tern (*Sterna lunata*) nests by Ruddy Turnstones at Laysan Island in the Pacific was so intense that Alexander Wetmore more than 90 years ago mentioned there being no chance for terns to breed until turnstones leave their wintering grounds (Olson 1996).

Ruddy Turnstones were also responsible for a big proportion of egg losses in a Spotted Sandpiper (*Actitis macularia*) population breeding near to a Common Tern colony in Leech Lake in Minnesota (Alberico *et al.* 1991), and they are perceived as important nest predators for Temminck's Stint (*Calidris temminckii*) in Finland too (Rönkä *et al.* 2006). Ruddy Turnstones can also occasionally predate nests of conspecifics as it was recorded at least once in Finland (Vuolanto 1968).

Turnstones are not only capable of exploiting unguarded nests, but they can purposefully attack incubating birds in pursuit of eggs. A quite dramatic story includes Ruddy Turnstones dragging the egg from beneath an incubating adult of Gray-backed Tern and devouring it directly next to the

Table 1. Inter and intraspecific predation among shorebirds. Species are ordered according to IOC World Bird List, ver. 6.3 (Gill & Donsker 2016).

Predator species	Prey species	Prey items	N of cases	Where	References
Eurasian Thick-knee (*Burhinus oedicnemus*)	Northern Lapwing (*Vanellus vanellus*)	Eggs; chick	1 ; 1	France[1]; UK	Cramp & Simmons 1983; Westwood 1983
Great Thick-nee (*Esacus recurvirostris*)	Kentish Plover (*Charadrius alexandrinus*)	Eggs	1	India	Dharmakurmarsinhji in Ali & Ripley 1981
Snowy Sheathbill (*Chionis albus*)	Snowy Sheathbill (*Chionis albus*)	Eggs[2]	Regularly	Antarctica	Jones 1963
Eurasian Oystercatcher (*Haematopus ostralegus*)	Northern Lapwing (*Vanellus vanellus*)	Eggs	1	Netherlands	Teunissen *et al.* 2008
Spur-winged Lapwing (*Vanellus spinosus*)	Black-winged Stilt (*Himantopus himantopus*)	Eggs	1	Greece	E. Makrigianni *pers. comm.*
Red-wattled Lapwing (*Vanellus indicus*)	Kentish Plover (*Charadrius alexandrinus*)	Eggs	1	UAE	Kosztolányi *et al.* 2009
Blacksmith Lapwing (*Vanellus armatus*)	Kittlitz's Plover (*Charadrius pecuarius*)	Chick	1	South Africa	Calf 2002
Blacksmith Lapwing (*Vanellus armatus*)	White-fronted Plover (*Charadrius marginatus*)	Eggs	At least 1	South Africa	Wiersma *et al.* 2018
Black-shouldered Lapwing (*Vanellus novaehollandiae*)	Northern Red-breasted Plover (*Charadrius aquilonius*)	Eggs or chicks	3	New Zealand	Wills *et al.* 2003
Black-tailed Godwit (*Limosa limosa*)	Northern Lapwing (*Vanellus vanellus*)	Eggs	1	Netherlands	Teunissen *et al.* 2008
Bristle-thighed Curlew (*Numenius tahitiesis*)	Grey Plover (*Pluvialis squatarola*)	Chick[3]	1	Alaska	C. Babcocks in Marks *et al.* 2002
Ruddy Turnstone (*Arenaria interpres*)	Eurasian Oystercatcher (*Haematopus ostralegus*)	Eggs	At least 1	Finland	Brearey & Hildén 1985
Ruddy Turnstone (*Arenaria interpres*)	Kentish Plover (*Charadrius alexandrinus*)	Eggs	Regularly; 1 ; 1	Portugal; Spain; China	A. Rocha *pers. comm.*; A. P. Hurtado *pers.comm.*; Ch. Huang *pers. comm.*
Ruddy Turnstone (*Arenaria interpres*)	Common Redshank (*Tringa totanus*)	Eggs	At least 1	Finland	Brearey & Hildén 1985
Ruddy Turnstone (*Arenaria interpres*)	Spotted Sandpiper (*Actitis macularia*)	Eggs	Regularly	USA	Alberico *et al.* 1991
Ruddy Turnstone (*Arenaria interpres*)	Ruddy Turnstone (*Arenaria interpres*)	Eggs	1	Finland	Vuolanto 1968
Ruddy Turnstone (*Arenaria interpres*)	Temminck's Stint (*Calidris temminckii*)	Eggs	At least 1	Finland	Rönkä *et al.* 2006
Black Turnstone (*Arenaria melanocephala*)	Red-necked Phalarope (*Phalaropus lobatus*)	Eggs	1	USA	Handel & Gill 2001

1) Country was assumed from the context (Cramp & Simmons, 1983)
2) Not directly observed but Snowy Sheathbills were only possible predators (Jones, 1963)
3) The chick was probably already dead (Marks *et al.*, 2002)
"at least 1" = context indicated more than one case possible, but it was not explicitly stated.

nest and pair of robbed terns (A. Wetmore in Bent 1929). Another narrative describes a situation when a group of Ruddy Turnstones attacked the nest of Sooty Terns (*Sterna fuscata*) and despite aggressive defence by parents, they reached and pecked the egg, which was later abandoned and left for the possible consumption by turnstones (Crossin & Huber 1970). Black Turnstones can be very aggressive too and adults were observed to jab their bills at an incubating Red-necked Phalarope (*Phalaropus lobatus*) which eventually fled and turnstones got the eggs (Handel & Gill 2001).

The strong, short and pointed bills of turnstones represent a clear advantage for egg consumption because these birds are able to open even albatross eggs (Marks & Hall 1992). Indeed, the egg-opening ability is important – as otherwise probably more species of shorebirds would occasionally incorporate energetically rich bird eggs into their diet. For example, Sanderlings (*Calidris alba*) were observed feeding on Royal Tern eggs, together with Ruddy Turnstones which were probably responsible for opening of the eggs (Loftin & Sutton 1979).

Egg predation behaviour in Ruddy Turnstone is probably spread by learning and watching other conspecific individuals opening eggs (Brearey & Hildén 1985). Therefore this behaviour can be patchy and unpredictable among turnstones (Loftin & Sutton 1979, Brearey & Hildén 1985, Farraway *et al.* 1986). Because high feeding specializations among individual Ruddy Turnstones are possible (Whitfield 1990), it is probable that effective individuals can play an important role in spreading egg predation behaviour among groups of turnstones. Such predictions could be readily testable with turnstones in aviaries using a simple experimental design.

Generally, turnstones are not perceived as predators by gulls and many terns (Brearey & Hildén 1985, Farraway *et al.* 1986), therefore they can be very successful egg predators (Brearey & Hildén 1985), occasionally causing large damage to breeding colonies of terns and gulls (Loftin & Sutton 1979, Brearey & Hildén 1985, Farraway *et al.* 1986, Olson 1996). More likely, rather than a new phenomenon, suggested by (Brearey & Hildén 1985), egg predation by turnstones is so scarce and regionally limited that the selection for perceiving turnstones as egg predators had not been strong enough to evolve adequate aggressive anti-predatory response in larids, often successfully performed against other avian predators (e.g. Cramp & Simmons 1983, Quinn & Ueta 2008, Sládeček *et al.* 2014). However, some tern species were observed to attack turnstones near their nests (Crossin & Huber 1970, Loftin & Sutton 1979, Brearey & Hildén 1985), which suggest probably more intense predator pressure from turnstones on terns in evolutionary time.

4.2. Curlews and godwits

Bristle-thighed Curlew (*Numenius tahitiesis*) on its wintering grounds at Pacific islands is well known for eating eggs of many seabirds including terns, boobies, noddies, shearwaters, petrels or frigatebirds (Ely & Clapp 1973, Marks & Hall 1992, Olson 1996). Exceptionally among shorebirds, Bristle-thighed Curlew can also use small stones for opening big albatross eggs (Marks & Hall 1992). Once a Bristle-thighed Curlew tried to swallow a Black-bellied Plover (*Pluvialis squatarola*) chick regurgitated by a gull in Alaska (C. Babcock in Marks *et al.* 2002). In the completely different environment of archipelagos in the middle of Pacific, though not directly confirmed, Bristle-thighed Curlews were likely responsible for egg predation in some nests of Tuamotu Sandpiper (*Prosobonia parvirostris*) at Tahanea atoll (D. Lank *pers. comm.*).

Bristle-thighed Curlews and Ruddy Turnstones are considered as performing egg predation behaviour predominantly during periods of other food shortage (Brearey & Hildén 1985, Marks *et al.* 2002), indicating opportunistic switch of prey or by a trial-and-error independent invention of egg-eating behaviour during the food shortage (Brearey & Hildén 1985). Indeed, Bristle-thighed Curlews caused more intense depredation of seabird nests at Laysan Island in the Pacific during the first half of 20th century in the period when island vegetation was nearly eliminated by European Rabbits (*Oryctolagus cuniculus*), which must have reduced insect availability for curlews considerably, in comparison with the 1990s (Marks *et al.* 2002).

Other curlews could be rare predators of other shorebirds as well, because the diet of Eurasian

Curlew (*Numenius arquata*) has occasionally contained young birds and possibly eggs (Van Gils *et al.* 2018), and Long-billed Curlew (*Numenius americanus*) was observed to predate on eggs and nestlings of Horned Lark (*Eremophila alpestris*) in Canada (Sadler & Maher 1976). Quite surprisingly, the invertebrate feeder, Black-tailed Godwit (*Limosa limosa*) was once recorded as the egg predator of Northern Lapwing (*Vanellus vanellus*) in the Netherlands (Teunissen *et al.* 2008), indicating that under intensive video surveillance, unexpected predatory and foraging behaviour can be recorded.

4.3. Lapwings and plovers

Lapwings are generally aggressive species (del Hoyo *et al.* 2020) and four species were involved as predators in five predation interactions with other shorebirds (Table 1). In the case of Blacksmith Lapwing (*Vanellus armatus*) predating on a Kittlitz's Plover (*Charadrius pecuarius*) chick, the non-breeding foraging lapwing entered the plover's territory and despite distraction display from plovers, after five minutes of aggressive behaviour, lapwing found, picked up, shook to death and swallowed one of two 2–3 days old plover chicks (Calf 2002).

In addition to the presented interactions, Black-shouldered Lapwing (*Vanellus novaehollandiae*) is a suspected egg predator of Chatham Oystercatcher (*Haematopus chathamensis*) based on the close presence of lapwings near oystercatchers nests during video monitoring (Moore 2014) as well as a predator of Southern New Zealand Dotterel (*Charadrius obscurus*) eggs according to camera pictures from Stewart Island (A. Burns & K. Carter *pers. comm.*). Pied Lapwing (*Hoploxypterus cayanus*) and Collared Plover (*Charadrius collaris*) were identified as predators of Sand-colored Nighthawk (*Chordeiles rupestris*) nests at sand beaches of Peruvian rivers in Amazon rainforest (Menezes & Marini 2017), which suggests that they could occasionally be a predator of shorebird eggs as well. Pacific Golden Plovers (*Pluvialis fulva*) were seen eating bird eggs on Laysan Island in the Pacific (Olson 1996).

4.4. Other species

Thick-knees (Burhinidae) have a varied diet with a small portion regularly consisting of vertebrates, namely small amphibians and reptiles (del Hoyo *et al.* 1996) but two species were recorded as exceptional predators of other shorebirds nests (Table 1). The second case of intraspecific predation was reported for Snowy Sheathbill (*Chionis albus*) from islands near the Antarctic Peninsula. The only suspected predators for the missing eggs were the breeding birds themselves or other sheathbills (Jones 1963). Sheathbills are omnivorous generalists, which is essential in the harsh environment of Antarctic and sub-Antarctic islands. Eggs and chicks of other seabirds, especially penguins, represent an important part of sheathbills' diet (del Hoyo *et al.* 1996), and other sheathbills, specifically non-breeders are assumed as principal egg predators of conspecifics (Jones 1963).

Intraspecific predation is also probable in Black-faced Sheathbill (*Chionis minor*) at Marion Island (Burger 1979). It was noted that Eurasian Oystercatcher (*Haematopus ostralegus*) can occasionally eat eggs and nestlings of other birds (Dement'ev & Gladkov 1969), namely gulls and terns (Cramp & Simmons 1983), or duck eggs (Jones 2008), therefore it is expected that they can occasionally predate on other shorebirds nests as well (Table 1). Given the strong bill capable of egg-opening and the fact that several species of oystercatchers from Southern hemisphere are understudied in comparison with North hemisphere relatives (Ens & Underhill 2014), it is possible that other species of oystercatchers can also occasionally eat eggs of shorebirds.

4.5. Conclusions

Taken together, the very diverse foraging tactics of shorebirds involve consumption of each other as well, though representing only a small proportion of the diet. Generally larger and more aggressive species of shorebirds are better predisposed to become predators of the eggs or chicks of other shorebirds. Regular bird nest predators among shorebirds with regionally significant impact on reproductive output of the prey species are Ruddy Turnstone and Bristle-thighed Curlew. The

pointed short bill of turnstones represents a useful tool for egg-opening and the fact that turnstones are not often recognized by prey species as potential predators help them to predate effectively on bird eggs. The prevailing anecdotal nature of the evidence for predation behaviour among shorebirds and generally less known diet of tropical shorebirds suggest that such behaviour can be occasionally performed by more species, especially in the tropics and thus contribute to the already highly variable life history strategies of shorebirds.

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Katsausartikkeli lajienvälisestä ja -sisäisestä saalistuksesta kahlaajilla

Saalistuspaine on usein yksi tärkeimmistä populaatiokokoa ja -dynamiikkaa määräävistä tekijöistä, ja sen merkitys on voi olla jopa lisääntymässä ihmisen toiminnan ansiosta. Vaikka peto–saalisvuorovaikutusta on tutkittu paljon, on vielä lajiryhmiä, joissa saalistajan käyttäytymisen merkitys ymmärretään vielä huonosti.

Tässä katsausartikkelissa selvitän saalistuskäyttäytymistä kahlaajalintujen keskuudessa: tämä koskee 16 tapausta lajienvälisestä saalistuksesta ja kaksi tapausta lajinsisäisestä saalistuksesta kahlaajissa, yhteensä 11 saalistajalajia ja 13 saalislajia. Saalistajat ovat yleensä kooltaan suurempia ja aggressiivisempia kuin saalislajit. Vastoin aiempia yksittäishavaintoja, karikukko ja alaskankuovi näyttävät olevan huomattava uhka rannikkojen pesimälinnustolle. Munien tuhoaminen voi pahimmillaan aiheuttaa kokonaisten lokki- ja tiirakolonioiden pesintöjen epäonnistumisen. Molemmilla lajeilla on terävä nokka, joka mahdollistaa munien rikkomisen. Alaskankuovi voi myös käyttää kiviä. Karikukkoja ei lokkikolonioissa ole koettu saalistajaksi, joten ne pystyvät helposti käyttämään munia hyödykseen.

Tämän katsausartikkelin tulokset viittaavat siihen, että (i) kahlaajat ja rantalinnut, joiden on oletettu lähinnä saalistavan selkärangattomia, voivat olla huomattavia petoja lajitovereilleen (ii) tällainen käyttäytyminen voi olla luultua yleisempää, ja mahdollisesti havaittavissa myös muissa lajiryhmissä. Tulokset lisäävät ymmärrystämme ravintoverkkojen monimutkaisuudesta.

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