



New evidence of a fish–bird interspecific feeding association between the European seabass and the European shag in the Mediterranean Sea

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Received: 3 February 2021 / Accepted: 27 April 2021
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Abstract Although they have received little attention, interspecific feeding associations are a particular predation behavior in which two or more different species temporarily feed simultaneously on the same food sources to obtain greater success in predation. These collaborations can be either mutualistic, commensalistic, or parasitic. One of the best-known examples is the seabird–cetacean associations. Prey herding is the foraging tactic most used in these associations and consists of swimming around and

under prey balls to trap them in the water column. Here we reported some new evidence of a fish–bird interspecific feeding association between the European seabass, *Dicentrarchus labrax* (Linnaeus, 1758) and the European shag, *Gulosus aristotelis* (Linnaeus, 1761). We analyzed this association through the photograph and video documentation provided by “citizen scientists” in the Mediterranean Sea. We collected reliable proofs of this behavior, at least, in three instances from observations made by recreational fishermen in the Kvarner bay (Croatia, North Adriatic Sea). From the photographs and videos made available, we attempted to reconstruct a predation strategy adopted by these associated species to better understand the advantage this provides during hunting. Although it is not yet clear whether this association is an opportunistic behavior of the European seabass or a mutualistic strategy used by both species to improve their catching success, this feeding association seems to increase the chances to defeat prey defense strategies. Notably, some behavioral imitation of hunting strategies may be put in place by seabasses, which often feed in association with dolphins and other birds using similar prey herding strategies.

Handling Editor: Sébastien Villeger

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10452-021-09868-z>.

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Keywords Mutualism · Predation · *Gulosus aristotelis* · *Dicentrarchus labrax* · Mediterranean Sea · Citizen science

Introduction

Positive interspecific associations have received less attention than the more studied antagonistic species interactions such as predation and parasitism (Leung and Poulin 2008; Stachowicz 2001; Palmer et al. 2019). Interspecific feeding associations (IFAs) represent a particular case in which individuals of two or more different species temporarily feed simultaneously on the same food sources. These associations can be mutualistic if both (or more) the species benefit, commensalistic if the facilitator is neither benefitted nor harmed, and parasitic when the host is used as a resource and harmed (Bronstein 2009). The mutualistic feeding association is a kind of “collaboration” between two, or in some cases more, different species in order to obtain greater success in predation (Jackson 1985; Minta et al. 1992).

Although there are numerous observations of interspecific feeding associations (Table 1), one of the best-known examples is the seabird–cetacean associations, which may involve many species. These interspecific associations would be predicted on the basis of the diets of the involved species. Most seabird–cetacean associations are probably opportunistic or incidental, as a result of a concentration of shared prey. Some species, however, may associate more regularly, and in these cases, it seems likely that seabirds obtain more benefits than other species (Evans 1982; Hebshi et al. 2008).

Prey herding is the foraging tactic of swimming around and under prey balls in an attempt to tighten or move them horizontally or vertically in the water column. This behavior is typical of interspecific feeding association and is particularly common among dolphin–bird associations (Wells et al. 1999; Connor 2000; Heithaus and Dill 2002; Vaughn et al. 2010). Usually, dolphins herd fish into dense concentrations near the surface, while birds take advantage and plunge into the shoals from aloft. Birds seem to initiate these associations by actively joining the dolphins (Quérouil et al. 2008). In fact, behavioral observations of birds following schools of non-feeding dolphins indicate that such associations are sometimes formed deliberately rather than merely opportunistically (May-Collado 2010). In most cases, the absence of benefit to the dolphins from these relationships led to the conclusion that they should be considered pure commensalism.

Several studies have described prey-herding behaviors in bird–cetacean associations (e.g., Würsig and Würsig 1980; Simila and Ugarte 1993; Clua and Grosvalet 2001). Here we document for the first time, to our best knowledge, evidence of a different interspecific feeding association between the European seabass, *Dicentrarchus labrax* (Linnaeus 1758), and the European shag, *Gulosus aristotelis* (Linnaeus 1761), in the Mediterranean Sea.

Material and methods

The evidence of the feeding association here described is based on previous observations made by recreational fishermen in the Kvarner bay (Croatia, North Adriatic Sea; an area where recreational fishing is not prohibited) and what we report here are the first photograph and video records of this interspecific feeding association. We collected reliable proofs of this behavior, at least, in three instances: i) in the sea of Lošinj Island (on September 7, 2017) where 4 seabasses followed a shag for few minutes though no observed successful hunt was documented; ii) in the sea of Rab Island (on October 3, 2018) where seabasses and a shag were observed hunting together; iii) in Krk Island (on October 27, 2019) where this feeding association was observed again (Fig. 1).

Results and Discussion

From our observations, we found that the feeding association involves only one shag but often two to four seabasses (Fig. 2a and b), and it starts when the shag and the European seabass meet in the same sea area of about 2–3 m² and the shag begins herding the prey (*Atherina* sp.) followed by the seabasses (Fig. 2c). Then, the shag dives underwater toward its preys, initially with the seabass behind it (Fig. 3a). This seems to mark the starting of the feeding association (Fig. 3b). Then, the shag and the seabasses separate, with the bird swimming in one direction on the surface and the seabasses in the opposite one in the deep inducing the formation of a prey ring (Fig. 3c). The continuation of this herding in opposite directions forces the preys to create a bait ball controlled by the seabasses, from the top and the bottom, in which the shag can dive (Fig. 3d). A bait ball is when small fish

Table 1 Examples of the diversity and geographic extent of feeding associations between species in the marine environment (and an example from freshwater)

Type of interaction	Predator 1	Predator 2	Other occasional predators	Preys	Geographic range	References
Birds–fish cetaceans and pinnipeds	Several species of birds	Dusky dolphin	Dogfish, thresher shark	Pilchard	Pacific Ocean	Vaughn et al. 2007
Birds–fish and cetaceans	Wedge-tailed shearwaters, brown noddies	Skipjack tuna, Dolphins	Dolphinfish, yellowfin tuna	Not specified fish	Pacific Ocean	Hebshi et al. 2008
Birds–cetaceans	Shearwater	Dolphins	–	Horse mackerel	Atlantic Ocean	Martin 1986
Birds–cetaceans	Terns, Hutton's shearwater	Dolphins		Not specified fish	Pacific Ocean	Bräger 1998
Fish–fish	Horse-eye jack	Spanish hogfish	Other labrid species, Yellow sea chub	Not specified fish	Atlantic Ocean	Silvano 2001
Fish–octopus	Grouper	Moray eel, Octopus	–	Not specified fish and invertebrates	Red sea	Diamant and Shpigel 1985
Birds–cetaceans and pinnipeds	Several species of birds	Cetaceans, pinnipeds	–	Sand eels and clupeoid fish	North Sea	Camphuysen and Webb 1999
Birds–cetaceans	Several species of birds	Dusky dolphin	–	Not specified fish	Atlantic Ocean	Degrati et al. 2014
Birds–cetaceans and fish	Cory's shearwater	Dolphins and Tunas	–	Not specified fish	Atlantic Ocean	Clua and Grosvalet 2001
Bird-bird	Dalmatian pelican	Great cormorant	–	Not specified fish	Lake Prespa	Crivelli and Vizi 1981

swarm in a tightly packed spherical formation as a defensive measure when they are threatened by predators (Vaughn et al. [2011](#)). Now the attack can proceed from three sides (Fig. [3e](#)), making the final attack more efficient for both species (Fig. [3f](#)).

From these observations, it is not yet clear whether this is an opportunistic behavior of seabass or a mutualistic strategy by both species to herd the school of fish in a shape that makes the attacks more effective (Supplementary Videos 1 and 2). Nonetheless, this feeding association seems to increase the chance to defeat prey defense strategies. The predators, in this case the shag and the seabass, try to force the fish school to the surface, herding it at the same time into a compact volume. The school of fish, trapped against the surface by the seabass and controlled by the shag above, loses its coordinated movement and becomes chaotic. Each prey fish, in attempts to save itself,

swims frenetic in all directions, and a compact bait ball forms as each fish scrambles to get away from the surface of the ball and hide in the interior (Hamilton [1971](#)). This sphere exposes the fewest fish on the surface to the predators, and it is usually effective to reduce predation. However, in case of a simultaneous and coordinated attack from the top and the bottom, as in the case of the feeding association between shag and seabass, this antipredatory strategy seems less effective.

This feeding association finds behavioral explanation in the ecology of the two species involved. The European seabass is a predatory species mainly feeding on small pelagic fish, including sardines, sprats, sand smelt and sand-eels, but also crustaceans and squids (Wheeler [1975](#); Pickett and Pawson [1994](#)). Juveniles tend to feed more on invertebrates than adults. This fish is an opportunistic predator and is

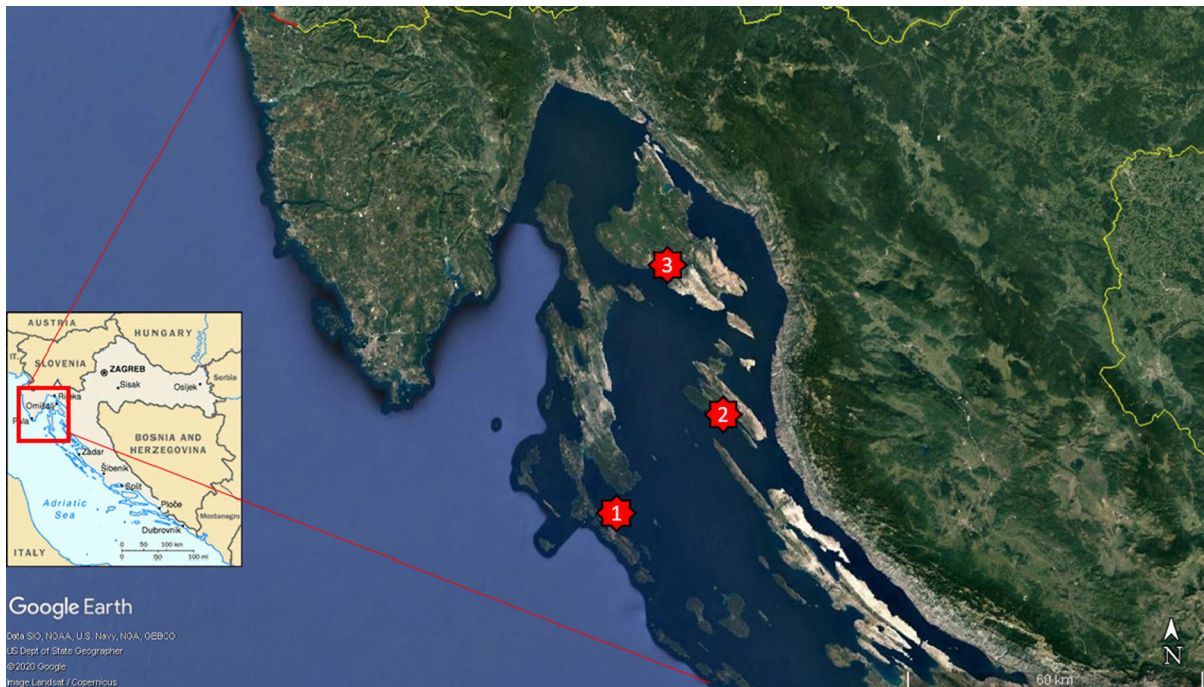


Fig. 1 Three locations in the Mediterranean Sea where the interspecific feeding association between the European seabass (*Dicentrarchus labrax*) and the European shag (*Gulosus aristotelis*) was observed during the last years

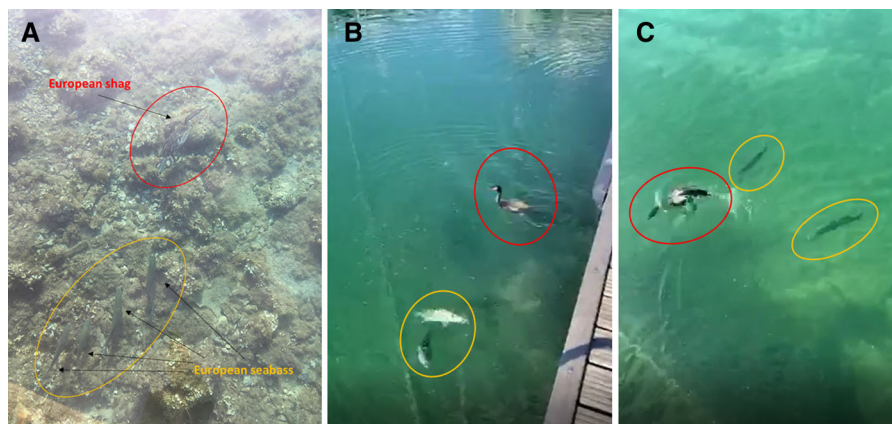


Fig. 2 The feeding association we observed involves only one shag at a time but often two to four seabasses (a). It starts when the two species are close enough (b), and a shag begins to follow

a school of small fish from the surface followed by seabasses in the deeper water (c)

known to attack prey species quite violently. Throughout their life, European seabasses develop a wide range of tactics to find and capture their prey. A typical tactic is to drive upwards toward the surface and attack from below at a steep angle. They tend to feed on whatever prey species are seasonally abundant in a particular location (Wheeler 1975; Pickett and Pawson

1994). In this way, the prey is not able to see the predator, but the contrast with water surface makes it more visible to the predator (Čech and Kubečka 2002; Jarolím et al. 2010).

The European shag feeds mainly on fish taken at the bottom or in mid-water, often foraging alone, while it is away from colonies (Michelot et al. 2017). This bird

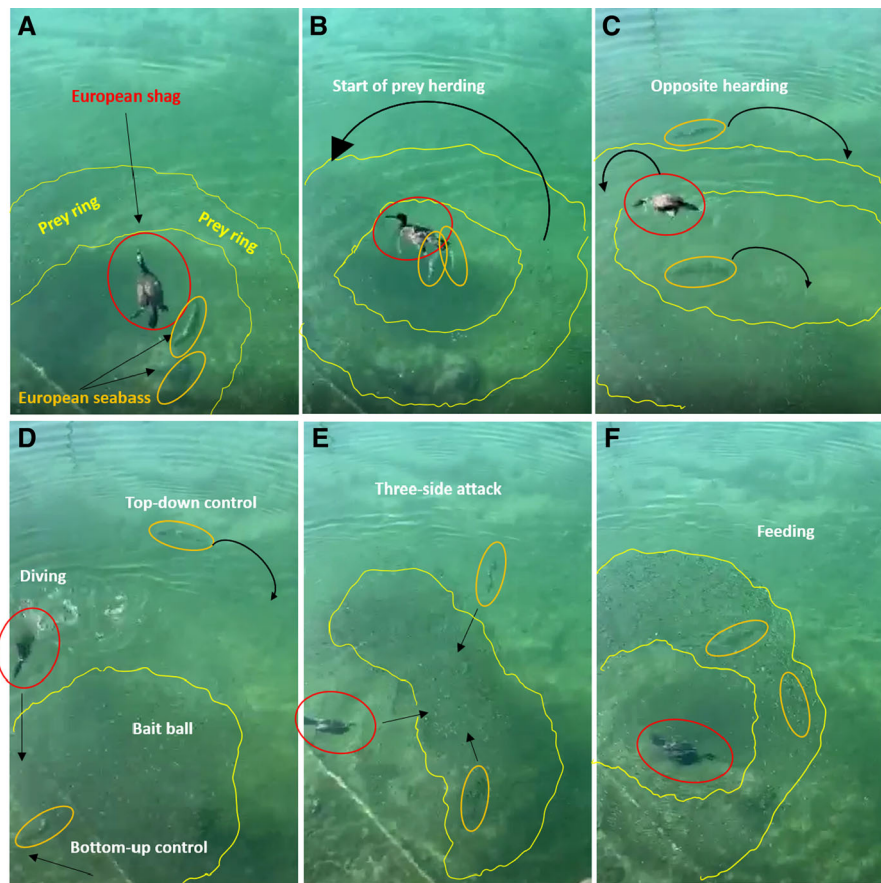


Fig. 3 This photograph sequence shows the behavior during the feeding association between the European shag (red circle) and the European seabass (orange circle). The association seems to start when the shag dives underwater toward its preys (yellow lines), initially with the seabass behind it (a). This initiates the prey herding (b) with the shag and the seabasses begin to swim

in two opposite directions inducing the formation of a prey ring (c). This creates a bait ball controlled by the seabasses, from the top and the bottom, in which the shag can dive (d). In this way, the simultaneous attack can proceed from three sides (e), allowing both species to prey easier (f). (Color figure online)

can also hunt shoals of fishes in very large flocks. The European shag feeds mainly during diving, and then, it pursues the prey underwater being able to dive up to about 95 s (Lea et al. 1996). The dives are alternated with periods of rest, depending on the duration of the dive, the depth of the dive, and the characteristics of the seabed. Because of these characteristics, this bird is often persecuted at fisheries and fish farms where it is considered as a pest for fish stocks (Carss and Marzano 2005) or becomes part of the bycatch (Velando and Freire 2002).

It would not be surprising that the behavior of the European seabasses in association with the European shag from our observations resembles that of dolphins in feeding association with other birds. In fact, as

mentioned before, seabass primarily targets small pelagic fish, most notably mackerel (*Scomber scombrus*), scads (*Trachurus* spp.), anchovy (*Engraulis encrasicolus*), and sardine (*Sardina pilchardus*). These four species also dominated the diets of common dolphins (Spitz et al. 2013). This overlap in feeding preferences is confirmed by the fact that dolphins are being caught by trawl fisheries in the Atlantic Ocean while feeding among seabasses (which causes a high rate of common dolphin bycatch observed in the pelagic trawl fishery for seabass; Spitz et al. 2013) and by the evidence that, also in the Mediterranean Sea, bottlenose dolphins were observed feeding on or together with seabass (Bearzi et al. 2009, 2010). Therefore, the similar diets and

bycatch of dolphins in the pelagic fishery for seabass suggest the simultaneous foraging of these two species. As a consequence, some behavioral imitation of hunting strategies could occur for the European seabass from dolphins, such as the prey herding we observed in the interspecific association with the European shag in the Mediterranean Sea.

Nonetheless, the exact foraging strategies of seabasses and shags are yet to be fully described, and the observations we reported here require further confirmations and experimental studies to be confirmed and shed more light on the ecological and evolutionary pressures underlying this behavior. However, as previous similar behavioral notes suggested (Palmer et al. 2019), the descriptions of these observations may inspire other researchers to add their collected evidence to the body of literature on interspecific associations to better investigate the mechanisms that promote these behaviors and to explore the consequences of altering these hunting strategies under anthropogenic pressures.

Finally, the evidence here reported shows once again that citizen science can play a crucial role in the discovery of new behaviors and ecological processes (Tiralongo et al. 2019). It is, therefore, important to strengthen the collaboration between researches and “citizen scientists,” such as sea users, because these observations represent an opportunity of access to a great amount of potentially interesting data.

Acknowledgements We thank Luka Nolden and Nejc Kotar for providing photographs and videos and making them available for our analysis and publication.

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